FRED Reports

SUMMARY OF SOCKEYE SALMON
(*Oncorhynchus nerka*) INVESTIGATIONS
IN TUSTUMENA LAKE, 1981-1991

by
G. B. Kyle

Number 122

Alaska Department of Fish & Game
Division of Fisheries Rehabilitation,
Enhancement and Development

SUMMARY OF SOCKEYE SALMON (Oncorhynchus nerka) INVESTIGATIONS IN TUSTUMENA LAKE, 1981-1991

by
G. B. Kyle

Number 122

Alaska Department of Fish and Game
Division of Fisheries Rehabilitation,
Enhancement and Development

Carl Rosier
Commissioner

J. P. Koenings
Director

P. O. Box 25526
Juneau, Alaska 99802-5526

May 1992

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES (continued)

LIST OF TABLES (continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF APPENDIX FIGURES

ABSTRACT

In 1981, the Alaska Department of Fish and Game and the United States Fish and Wildlife Service cooperatively initiated new and expanded fishery and limnological investigations in Tustumena Lake. These studies were designed to characterize sockeye salmon (*Oncorhynchus nerka*) production in glacially-influenced Tustumena Lake, and evaluate the stocking of hatchery-produced fingerlings relative to wild production. Sockeye salmon fingerlings were first released in Tustumena Lake from Crooked Creek Hatchery in 1976, and have been stocked almost every year since then. The initial working hypothesis of sockeye salmon production in this lake, as in the majority of other sockeye-producing lakes, followed the classical approach of the stock-recruitment theory. This approach is predicated on density-dependent fry recruitment and resultant effects on subsequent stock size under assumed conditions of a stable rearing environment. However, changing environmental conditions during lake rearing can confound stock-recruitment/density-dependent relationships. For example, the broodyear that produced the highest smolt biomass occurred during the period of high stocking (~16 million), but from a lower escapement compared to broodyears before and after the broodyear of highest smolt biomass when stocking levels were similar. Moreover, wild smolt biomass in Tustumena Lake for broodyears 1979-1988 was not significantly ($p > .05$) related to the number of spawners, and similarly, hatchery smolt biomass (release years 1980-1989) was not significantly ($p > .05$) correlated to the number of fingerlings planted. In addition, zooplankton biomass was not significantly related to numbers of sockeye juveniles rearing in the fall. These findings are inconsistent with unconditional density-dependent sockeye production. Furthermore, a preliminary evaluation of the effects of diverse rearing environments on age-1 smolt production during six parent years (1979-1984), when numbers of spawners were relatively consistent, revealed relationships characteristic of density-independent production. That is, environmental variables (e.g., seasonal precipitation, lake temperature, onset of spring heating) accounted for most (84-94%) of the inter-annual variation in wild age-1 smolt production in Tustumena Lake. Thus, sockeye production in Tustumena Lake appears to be primarily influenced by environmental variables over the effects of fish density; however, there could be subsequent density-dependent effects resulting from poor environmental conditions.

INTRODUCTION

Studies related to sockeye salmon (*Oncorhynchus nerka*) production in Tustumena Lake began with sonar enumeration of adult escapements in 1968. During 1968-1991 a wide variety of sockeye salmon studies were done in Tustumena Lake to evaluate production parameters such as in-lake juvenile growth, adult spawner distribution among the major tributaries, and optimum escapement levels (Table 1). Sockeye salmon fingerlings were first released in Tustumena Lake from Crooked Creek Hatchery in 1976, and with the exception of 1977, have been stocked every year since then. In 1981, the Alaska Department of Fish and Game (ADF&G) and the United States Fish and Wildlife Service (USF&WS) cooperatively initiated new and expanded fishery and limnological investigations. These studies were conducted to determine factors affecting the capacity of Tustumena Lake to produce sockeye salmon and to select an appropriate annual stocking level respective to avoiding negative impacts to the natural stock.

Initially, the working hypothesis of sockeye salmon production in Tustumena Lake was that this system operated in a density-dependent fashion where fluctuations in smolt production are directly related to sockeye salmon density. That is, with density-dependent production, the variability in smolt production (juvenile rearing success) is related to density-related responses in freshwater trophic levels (Foerster 1944; Johnson 1965; Brocksen et al. 1970; Koenings and Burkett 1987; Kyle et al. 1988). However, if juvenile fish density is not sufficient to challenge the limnetic forage base, trophic-level responses become uncoupled from fish production and correlated to environmental variables (density-independent). In Tustumena Lake, a preliminary analysis suggests that sockeye salmon production is primarily density-independent as environmentally-dependent variables were responsible for 84-94% of the annual variation in the production of wild age-1 smolts during parent years 1979-1984 (Koenings et al. 1988).

Table 1. Description of sockeye salmon evaluation activities conducted on Tustumena Lake.

Activity	General description	Activity	General description
Adult Sonar	Sonar enumeration of sockeye escapement in the Kasilof River. Includes sampling of fishwheel catches at sonar site for age, weight, length, and sex composition. Done annually from mid-May to mid-August.	Smolt Enumeration and Sampling	The use of traps in the Kasilof River to capture smolt for out-migration estimates and timing, age-weight-length composition, and hatchery contribution of smolts. Done from mid-May to early July.
Townet Surveys	Sampling of juvenile fish for species composition, size, and age in Tustumena Lake. One to three surveys have been done during June-October.	Limnology Surveys	Sampling at three permanent Stations in Tustumena Lake to measure primary and secondary productivity. Monitoring of standing crop and species composition of phytoplankton and zooplankton, and measuring parameters such as temperature, dissolved oxygen, alkalinity, and light penetration. Sampling once each month during May-October.
Spawning Ground Surveys	Ground surveys of seven major tributary streams to determine distribution of spawners among the major tributaries. Three surveys per tributary are done during August.	Hydroacoustic Surveys	Estimations of juvenile sockeye abundance and fish distribution. Townet sampling is done in conjunction with hydroacoustic surveys for identification and sampling of targets. One to three surveys have been done each year.
Egg-Take and Fry Stocking	Collection, fertilization, and incubation of eggs at Crooked Creek Hatchery and the stocking of fingerlings in Bear and Glacier Flats Creeks or in Tustumena Lake. Eggs are taken in mid-August and fry are released in June.	Genetic Sampling	Collection of muscle, liver, and eye tissue for gel electrophoresis. Identification of biochemical genetic variants among spawning stocks.
Stock Separation	In-season sampling of commercial sockeye catches in Cook Inlet, and apportionment of the catch to respective river systems on the basis of scale pattern analysis and age, weight, and length characteristics.	Emergent Fry Sampling	Sampling of emergent sockeye fry migration timing from Glacier Flats and Bear Creeks. Conducted on weekly basis from early-April to mid-June.

During 1981-1986, preliminary findings of sockeye salmon investigations conducted in Tustumena Lake have been summarized in annual progress reports (Van Ray et al. 1983; Tarbox et al. 1984; Flagg et al. 1985, 1986 and 1987). In addition, results of sockeye salmon investigations supported by the Anadromous Fish Conservation Act for the years 1987-1991 are presented in annual reports (Kyle 1987, 1988a and 1989; Shields and Kyle 1990; Todd and Kyle 1991). The purpose of this report is to 1) provide a description of the methods and techniques used to assess sockeye salmon production in Tustumena Lake, 2) provide a summary of the results of hatchery releases of sockeye salmon fingerlings, including wild and hatchery smolt and adult production for the years 1981-1991 (and pertinent data beforehand), 3) present a summary of limnological data collected during 1981-1991 to characterize lake productivity, 4) provide a cursory assessment of factors influencing sockeye salmon production in Tustumena Lake, 5) present in one document all pertinent lake productivity information and data for review by ADF&G and the USF&WS, and finally 6) to consider converting the stocking of sockeye fingerlings into Tustumena Lake from an applied research activity to an annual production project.

Description of Study Area-- Tustumena Lake (60° 10'N, 150° 55'W) lies within the boundaries of the Kenai National Wildlife Refuge located on the Kenai Peninsula in southcentral Alaska (Figure 1). This lake has a surface area of 294.5 km^2 (73,942 acres), is approximately 40 km long, 8 km wide, and is 33 m in elevation. The mean depth is 24 m and the maximum depth is 320 m. The lake is fed by several clear-water streams and two glacial streams which originate in the Harding Icefield.

The lake is oligotrophic, with a mean May-October total phosphorus (corrected for turbidity and inorganic phosphorus) concentration of 3.7 μg/L, a total Kjeldahl nitrogen concentration of 155 μg/L, and a chlorophyll a concentration of 0.45 μg/L. The lake is turbid (40-48 NTU) with glacial silt and consequently

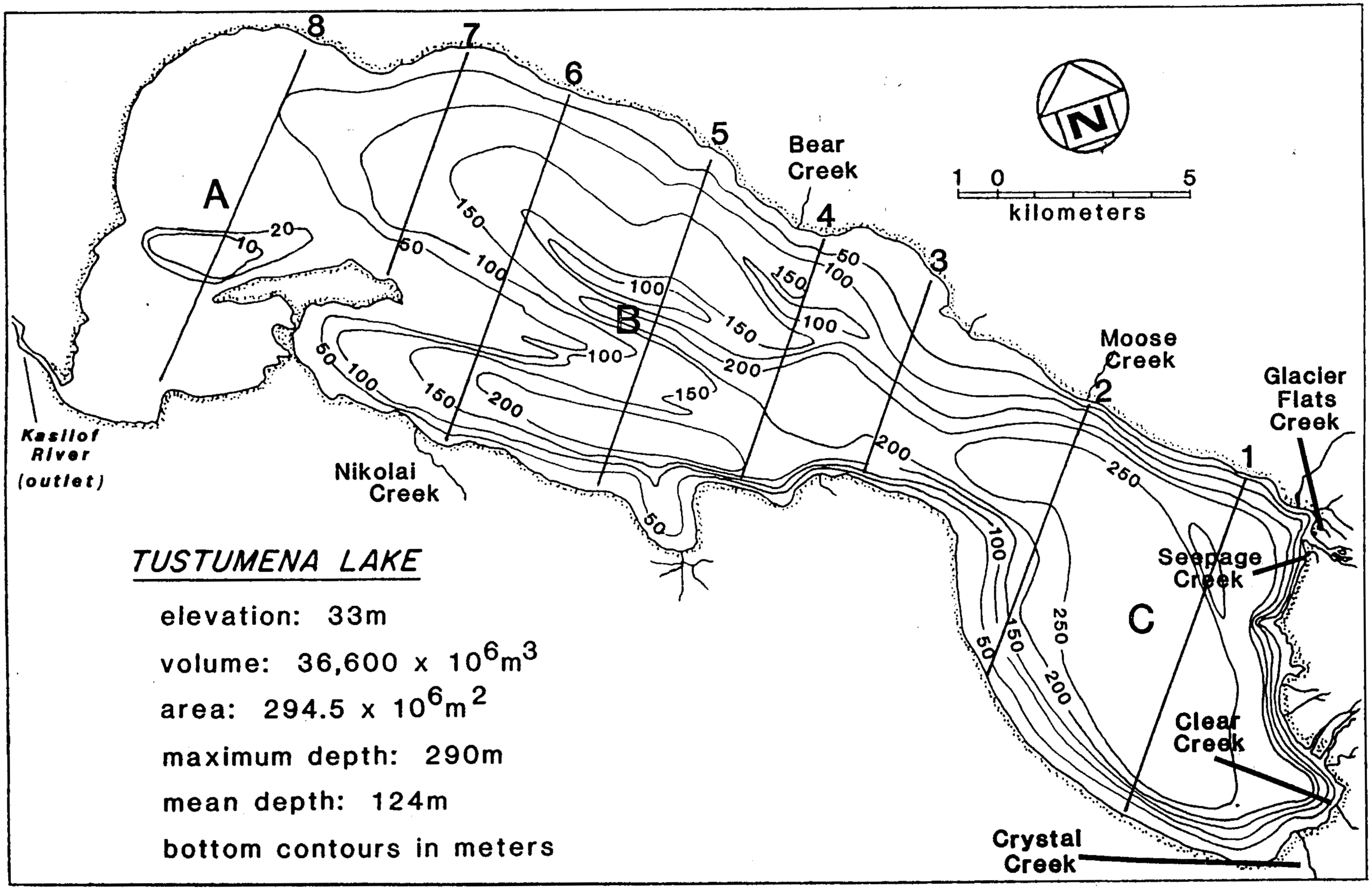


Figure 1. Morphometric map of Tustumena Lake showing the location of limnological sample stations (A-C), transects used for hydroacoustic surveys (1-8), and the seven major salmon-producing tributaries.

light penetration is limited to the upper 2 m and the euphotic zone is less than 1% of the lake's volume. The zooplankton community consists of two copepods, *Diaptomus pribilofensis* and *Cyclops columbianus*. All five species of Pacific salmon are found in the Tustumena Lake system; however, mainly sockeye salmon utilize the limnetic area of the lake. Sockeye salmon returning to the Tustumena Lake system contribute an average of 30% of the total sockeye salmon harvested in the upper Cook Inlet commercial salmon fishery each year. Resident fish species include rainbow trout (*Oncorhynchus mykiss*), lake trout (*Salvelinus namaycush*), Dolly Varden char (*Salvelinus malma*), threespine stickleback (*Gasterosteus aculeatus*), coastrange and slimy sculpin (*Cottus aleuticus* and *cognatus*), and round whitefish (*Prosopium cylindraceum*).

METHODS

Egg Takes-- Sockeye salmon eggs have been taken from returning adults at Glacier Flats, Bear, and Seepage creeks since 1974. In most years, egg takes were conducted at both Glacier Flats and Bear creeks. Each year sockeye salmon adults were passed daily through picket weirs at the creeks starting in early August until escapement goals were reached (5,000-10,000 Glacier Flats Creek; 25,000 Bear Creek). After achieving the escapement goals in each creek, ripe adult sockeye salmon were held at the weirs, and eggs were taken daily for approximately 10 days. After fertilization and water hardening, sockeye salmon eggs were flown to the Crooked Creek Hatchery located near Kasilof, Alaska and seeded in incubators for egg development. The egg take, fecundity sampling, and culturing protocol followed procedures outlined in the ADF&G Fish Culture Manual (FRED Staff 1983). Policies pertaining to protection of genetic integrity of wild stocks were followed (Davis 1985).

Fingerling Releases and Emergent Fry Sampling-- Hatchery-produced sockeye salmon fry were reared 4-6 weeks at the Crooked Creek Hatchery until they reached approximately 0.20 g before being stocked as fingerlings in Tustumena

Lake. Each year, approximately 2% of the stocked fingerlings were marked by removal of a ventral fin (right ventral [RV] for the Glacier Flats Creek stock and left ventral [LV] for Bear Creek stock) so that the number of hatchery-produced smolts and returning adults could be estimated. In 1984 and 1985, mark mortality was evaluated by releasing an equal number of fingerlings with an adipose clip (control group) and a ventral clip (treated group). In 1984 an equal number of fingerlings were marked with a right ventral clip and an adipose clip (Glacier Flats Creek stock). In 1985, the experiment was repeated using an equal number of fingerlings marked with a left ventral clip and an adipose clip (Bear Creek stock). A differential mark mortality factor (DMF) for these fingerlings was determined by comparing the number of ventral- and adipose-clipped fish that migrated as smolts and returned as adults.

Sockeye salmon fingerlings were released during mid-June of each year. During 1976-1985 respective fingerlings were transported and planted directly in Bear Creek and Glacier Flats Creek using a modified fire-fighting bucket slung from a helicopter. Beginning in 1986, a fixed-wing aircraft was used to air-drop respective fingerlings near the mouth of each creek. Hatchery fingerlings released from Crooked Creek Hatchery and wild fingerlings (caught in the lake near the release sites) were sampled for size at time of stocking for comparison. Fingerlings were measured from snout-to-fork of tail to the nearest millimeter and weighed to the nearest 0.01 g.

Sampling of emergent sockeye salmon fry entering Tustumena Lake from Bear and Glacier Flats creeks was conducted during mid-April until mid-June of 1988 to determine the timing of peak migration. Weekly sampling was accomplished using a small-mesh (0.5 cm) fyke net with 8-m wings attached to a live box. All fish captured were enumerated during each sampling period. The nets initially sampled the entire volume of both creeks during the period of 2000-0800 h. However, beginning in late May, the creek discharge and debris loading in Bear Creek became excessive and subsampling was conducted.

Consequently, catches in Bear Creek during the last three sample trips (31 May, 8 June, and 15 June) were expanded according to the proportion of the total creek discharge that was subsampled. Catches were converted to catch-per-unit-effort and mean weight of emergent fry was recorded to the nearest 0.01 g.

Hydroacoustic/Townet Surveys-- Beginning in 1981 hydroacoustic surveys were conducted to assess juvenile sockeye salmon abundance and distribution. During 1981-1983 surveys were done three times between June and October in an effort to estimate mortality over the summer growing season. Beginning in 1984, the early survey (June) was eliminated because incomplete fry recruitment in the lake prior to this survey made it impossible to accurately estimate mortality between this survey and subsequent ones. Because of funding restrictions, and finding fry entering the lake after July, only the late-September survey was conducted each year beginning in 1988.

Hydroacoustic surveys comprised of recording data along transects perpendicular to the longitudinal axis of the lake (Figure 1). Flashing construction lights were placed at both ends of each transect to assist in maintaining transect course. Since 1989, LORAN and compass headings were used to maintain course. Initially, eight transects were chosen to represent all areas and basins of the lake (systematic sampling design). More recently (1990-1991), the lake was divided into three equal areas and three transects were selected randomly in each area for sampling. Recording of down-looking acoustic data along the transects was done at night because juvenile sockeye salmon are more evenly dispersed. In the early surveys (1981-1988), two series were conducted such that recording along the transects was done twice (on different nights). Since 1989, one series of eight to nine transects was recorded for analysis. Transect speed was 2.0-2.6 m/sec with the exception of 1983 when speeds were increased to evaluate if increased transect speed would reduce the variability associated with the length of time (8 hours) required to complete a survey series. This technique proved to be inappropriate because of significant changes in target resolution and was abandoned.

The type of hydroacoustic equipment used each year varied as new equipment and technology became available. In general, a Simrad® EK-120 echosounder with a 9° single-beam transducer and reel-to-reel recorder was used during 1981-1983. Beginning in 1984, a BioSonics 101 echosounder with either a 15° single-beam or 6/15° dual-beam transducer was used. Since 1988, a BioSonics 105 echosounder was used. Fish signals were recorded using a digital cassette recorder beginning in 1984. With both types of equipment, fish signals were also recorded on paper with a compatible chart recorder.

Analysis of recorded hydroacoustic data was conducted under contract by Dr. Richard Thorne of BioSonics Inc. (formerly of the University of Washington - Fisheries Research Institute) as described by Kyle (1990). Fish densities were low enough that echo counting techniques (Thorne 1983) could be used. The numbers of echoes from fish were counted in 10-min increments along transects and in 5 depth intervals (2.5-5, 5-9.5, 9.5-15.5, 15.5-27.5, and 27.5-38 m).

Sampling volumes were estimated by the duration-in-beam technique (Nunnallee and Mathisen 1972; Nunnallee 1980; Thorne 1988). For each depth strata and 10-min increment, transect fish densities (no./m^3) were summed to determine the total areal density (no./m^2) of fish for each transect series. Mean transect fish densities were weighted by time, since end-of-transect increments were usually less than 10 min. A mean areal fish density and an associated variance was computed for each transect from the two transect series. If only one transect series was conducted, the fish density and variances were

---

® Mention of commercial products and trade names does not constitute endorsement by ADF&G, FRED Division.

computed by collapsing adjacent transects into a strata as described by Bazigos (1976).

Fish population estimates were obtained by multiplying the lake area representing each transect or collapsed strata by the calculated fish density for that respective transect or strata. Transect or strata variances were summed and a 95% confidence interval for the total fish population estimate was calculated for each survey (Thorne and Thomas 1982). Finally, fish population estimates in the surface to 2.5 m strata (undetected zone in the down-looking mode) was estimated by extrapolation of fish densities in the 2.5-5.0 m strata. However, during the early and mid-summer surveys of 1983-1986, data from up-looking deployment of the transducer was used to adjust the extrapolated fish densities in the surface to 2.5 m depth strata.

Identification of acoustic targets as to species and cohorts was made using a 3 x 3 m townet as described by Gjernes (1979). Since 1982, at least one 20-min net tow per hydroacoustic transect was directed by the acoustic operators to sample specific concentrations of fish targets. Townet catch compositions, usually by transect, were used to apportion the total fish population into estimates of age-0 and age-1 sockeye. A 95% confidence interval was calculated for age-0 and age-1 sockeye salmon after Thorne and Thomas (1982).

Sockeye juveniles collected by townetting in 1983, 1985, 1987, and 1988 were analyzed for foregut content. Stomachs of at least 20 juveniles per year were preserved in a vial containing 10% neutralized formalin for analysis. The stomach contents of each fish were identified, and zooplankton prey were measured for body size as described in Koenings et al. (1987). Replicate zooplankton samples from lake basin stations were used to calculate the electivity index (Ivlev 1961) to determine the feeding selectivity of juvenile sockeye on different taxa of macro-zooplankton. In addition, this index was used to determine size-selectivity of the two copopods consumed by juvenile sockeye.

Smolt Outmigration Estimates and Sampling-- Canadian fan traps (Flagg 1983) were used during 1981-1984 in the Kasilof River to capture, enumerate, and sample sockeye salmon smolts. Beginning in 1985, two types of smolt traps were used; in shallow water (<1 m) Canadian fan traps were used while in deeper water (>1 m) incline-plane traps were operated (Kyle 1983). Live boxes were attached to the downstream end of each trap to facilitate enumeration and age-weight-length (AWL) sampling. Smolt enumeration and AWL sampling commenced each year at the start of the migration in early- to mid-May and continued until late-June or early-July. All fish captured by the traps were enumerated by species and released daily. In addition, approximately 2,000 smolts were examined each day for hatchery fin clips, and 20 smolts per day were anesthetized in an MS-222 solution, for measurements of snout-to-fork length (nearest millimeter) and weight (nearest 0.1 g). A scale smear was taken from each of the 20 smolts sampled each day to determine age. Mean lengths and weights for each age group were weighted by multiplying the subsample length and weight for each sampling period (week) by the number of smolts outmigrating during the sampling period, summing all products, and finally dividing by the total population estimate of each age class.

Population estimates of the number of sockeye salmon smolts migrating from Tustumena Lake each year were made using weekly trap efficiencies determined through a mark-and-recapture procedure (Rawson 1984). Briefly, the procedure involved staining 500 smolts each week of the migration with Bismark Brown dye solution (1 g/30 L water) and releasing them approximately 2 km upstream of the smolt traps. Weekly migrations were estimated from the recovery of stained smolts to determine trap catch efficiency. The percentage of the total migration comprised of age-1 and age-2 smolts was estimated for each weekly period using scales obtained from samples collected that week. This percentage was then applied to the estimated total smolt migration for the weekly period to obtain estimates of the number of migrating smolts for each age class (Flagg et al. 1984).

The number of hatchery-produced sockeye salmon smolts migrating each year was estimated from the proportion of marked-to-unmarked smolts recovered during sampling, and the expansion of the recovered marked smolts by the percentage marked for that respective release year (Reed 1981). In addition, the number of hatchery smolts produced each year was adjusted by a 1.5 differential mark mortality factor (DMF), determined as previously described.

Adult Returns, Spawner Surveys, and Adult Sampling-- Since 1968, sonar equipment has been used on the north and south banks of the Kasilof River to estimate the total number of adult sockeye salmon migrating into Tustumena Lake. Usually the sonar units were installed the first week of July and removed by mid-August of each year. Estimation of the number of adult sockeye salmon migrating before and after deployment of the sonar units were extrapolated from daily escapement proportions during years when the sonar gear was operating earlier and later than other years. Procedures for deployment, operation, and calibration of the side-scanning sonar equipment are summarized in Tarbox et al. (1983).

Fishwheels and sometimes beach seines or drift gillnets were used to determine the salmon species composition of sonar counts, and to obtain size and age samples of returning sockeye salmon. Species apportionment of sonar counts were grouped into samples of at least 150 salmon. The daily sonar count was multiplied by the proportion of adult sockeye in the catch to obtain the estimated sonar count.

The total commercial harvest of Tustumena Lake sockeye salmon in the mixed-fishery of Cook Inlet was determined by linear discriminant analysis of scale patterns combined with age composition and size data (Cross et al. 1987). Escapement samples provided scales of known origin to construct linear discriminant functions. Sockeye salmon scales from commercial catches throughout the fishery were classified with discriminant functions to estimate the contribution by age groups of sockeye salmon bound for Tustumena Lake. Since 1987, harvest of sockeye salmon bound for Tustumena Lake was based on age-component analysis without using linear discriminant analysis (Dave Waltemyer[1] pers. comm.).

Harvests of Tustumena Lake sockeye salmon in the dipnet and gillnet personal-use fisheries were estimated from creel estimates and on-site monitoring of catches, respectively. Sport harvest of Tustumena Lake sockeye was obtained from the statewide harvest survey.

The relative distribution of spawning adult sockeye salmon among the major tributaries of Tustumena Lake was determined each year by utilizing a combination of weirs, ground surveys, and aerial surveys. As previously mentioned, weirs were operated annually on Glacier Flats and Bear creeks. Ground surveys were also conducted at Glacier Flats and Bear creeks each year after the weirs were installed to determine upstream escapement. Peak sockeye salmon counts on the other major spawning tributaries (Moose, Seepage, Crystal, Clear, and Nikolai creeks) were conducted annually by ground or aerial surveys. During most years, three ground surveys were conducted on each tributary during the peak of migration (early-mid August). Ground surveys required at least two observers; one for counting live fish and one for counting dead fish. Due to the range of spawning in Nikolai Creek (>20 km), aerial surveys (helicopter) were conducted to obtain peak counts. Spawners in a measured section of Nikolai Creek were simultaneously aerial surveyed and counted by a ground survey to calibrate the aerial counts.

---

[1]ADF&G, 34828 K-B Road, Soldotna, AK 99669.

Age compositions of sockeye salmon returning to Glacier Flats and Bear creeks were determined by aging otoliths. Each year a total of 100-500 fish were sampled from each creek during operation of the weirs. In addition, these sockeye salmon were measured for mean weight (nearest 0.1 kg) and mideye-to-fork length (nearest 0.5 cm).

During 1986-1988, 60 sockeye salmon were sampled each year from the major tributaries for identifying biochemical genetic variants among the spawning stocks. The intent of this sampling was to determine if there was significant variation in allelic frequencies to indicate stock heterogeneity. Earlier testing indicated no significant genetic variation among sockeye salmon stocks of Tustumena Lake (Grant et al. 1980). Samples of eye, muscle, and liver tissue were collected from sockeye salmon spawners and frozen for analysis. In 1986 and 1987, samples were collected by ADF&G personnel and sent to the ADF&G Genetic Laboratory in Anchorage. In 1988, samples were collected by USF&WS and ADF&G personnel, and the samples were forwarded to the USF&WS Genetic Laboratory in Anchorage. The 1986 samples spoiled due to an undetected failure of a freezer and consequently were not analyzed. However, both the 1987 and 1988 samples were analyzed by the USF&WS laboratory in Anchorage.

Horizontal gel electrophoresis as outlined by Utter et al. (1974) was used to detect protein variants of the genetic samples. Detailed analytical and statistical procedures can be obtained from the USF&WS Genetic Laboratory in Anchorage (Dick Wilmot[2] pers. comm.). However, in general, banding patterns on the starch gel reflect allelic products with differences being detected by their mobility. The genetic nature of the variants (hetero vs homogeneity) are inferred from the observed banding patterns.

---

[2]USF&WS, 1011 E. Tutor, Anchorage, AK 99503.

Finally, adult sockeye salmon (1,000/day) were examined for missing fins at each of the weirs located on Glacier Flats and Bear creeks. Usually, between 10,000-20,000 sockeye salmon were examined annually for hatchery fin clips at each weir site. The marked-to-unmarked ratio was recorded and the original brood-year marking level was incorporated in the expansion of recovered marked adults to estimate the number of hatchery-produced adults. In addition, a 1.5 differential mark mortality factor (DMF) was calculated for returning adults returning from the mark-mortality experiment conducted on hatchery fingerlings released with ventral- and adipose-clipped fins in 1984 and 1985. The same estimated percentage of hatchery-produced fish contributing to the escapement was applied to the estimated harvest of Tustumena Lake sockeye salmon in the commercial, sport, and personal-use fisheries. The total number of hatchery-produced fish in the total return was the summation of hatchery-produced fish estimated in the escapement and the commercial, sport, and personal-use fisheries. In 1990 and 1991, the estimation of the contribution of adults returning to Tustumena Lake was based on the contribution of respective hatchery smolts migrating the system. This was done because it is believed that the aerial stocking of fry in the lake has caused a higher percentage of straying, especially of Bear Creek stock straying into Glacier Flats Creek, and the probable increase in lake spawning of hatchery-released fish.

Limnological Surveys-- Limnological sampling in Tustumena Lake was conducted at three stations to characterize the three lake basins (Figure 1) at 3-week intervals during the ice-free period. Lake temperatures and dissolved oxygen (DO) were measured at the three stations using a YSI model 57 temperature/dissolved oxygen meter. The algal light compensation point (euphotic zone depth) defined as the depth at which 1% of the subsurface light (400-700 nm) is available for photosynthesis (Schindler 1971), was determined using a Protomatic submersible photometer. Light measurements were taken at 0.25-m increments from the surface to 3 m, and a temperature/dissolved oxygen profile was taken at 1-2 m intervals from the surface to 50 m. Summer heat budgets were calculated for each rearing year after Koenings et al. (1987), and used to quantify the onset of spring, the seasonal mean water temperature, and date of maximum heating.

Both the epilimnetic and mid-hypolimnetic zones were sampled for algal nutrients (e.g., nitrogen, phosphorus, silicon, and carbon) and other water quality characteristics. All chemical and biological samples were analyzed according to procedures detailed in (Koenings et al. 1987). Briefly, alkalinity was determined by sulfuric acid (0.02 N) titration, and pH was measured using an Orion model 399A ionanalyzer. Filterable reactive phosphorus (FRP) was analyzed by the molybdate blue-ascorbic acid method of Murphy and Riley (1962) as modified by Eisenreich et al. (1975). Total phosphorus was determined by the FRP procedure after persulfate digestion. Nitrate and nitrite (NO_3+NO_2) were determined as nitrite, following the cadmium reduction of nitrate, and total ammonia was determined using the phenylhypochlorite procedure after Stainton et al. (1977). Total Kjeldahl nitrogen (TKN) was determined as total ammonia following sulfuric acid block digestion (Crowther et al. 1980). Finally, reactive silicon was determined using the ascorbic acid reduction to molybdenum-blue after Stainton et al. (1977).

Primary production (algal standing crop) was estimated by determining concentrations of the algal pigment chlorophyll a (chl a) using the fluorometric procedure of Strickland and Parsons (1972). The low-strength acid method recommended by Reimann (1978) was used to estimate phaeophytin. Nutrient and chl a samples (1-2 L) were filtered through 4.2-cm GF/F filters to which 1-2 mL of saturated $MgCO_3$ was added. Filters were stored frozen in plexiglass petrislides until analyzed.

Zooplankton were enumerated from duplicate 50-m vertical tows using a 0.5-m diameter (153-μm mesh) conical net. The net was pulled at a constant 1 m/s, and all organisms were preserved in a 10% neutralized formalin solution. Zooplankton were counted, using a dissecting microscope, from triplicate 1-mL subsamples taken with a Hensen-Stempel pipette, and placed in a 1-mL Sedgewick-Rafter cell. Copepods, the only taxa of zooplankton present in Tustumena Lake, were identified after Wilson (1959) and Yeatman (1959). Finally, zooplankton body sizes were obtained by measuring the length to the nearest 0.01 mm of at least 10 individuals along a transect in each 1-mL subsample (Koenings et al. 1987).

RESULTS AND DISCUSSION

Egg Takes-- During 1974-1991, over 280 million eggs were taken from Tustumena Lake sockeye (Table 2) to support stocking projects in Tustumena Lake and lower Cook Inlet lakes. Approximately 164 million were taken from Glacier Flats Creek, 115 million from Bear Creek, and nearly one million from Seepage Creek. The largest egg take occurred in 1985 (23.7 million) while the smallest (300,000) occurred in 1974. The average number of eggs taken at Glacier Flats Creek each year was 9.7 million and at Bear Creek was 8.2 million. The fecundity of Tustumena Lake sockeye salmon ranged from 2,991 to 3,710 eggs per female and averaged 3,271 (Table 3). In addition, the difference in mean fecundity of sockeye salmon from Bear Creek (3,158) and Glacier Flats Creek (3,358) was slight (6%).

Fingerling Releases and Emergent Fry Sampling-- During 1976-1991, a total of nearly 143 million sockeye salmon fingerlings were released from the Crooked Creek Hatchery into Tustumena Lake (Table 4). Of these, 86 million fingerlings were Glacier Flats Creek stock and 57 million were Bear Creek stock. Of the total number of fingerlings released, 2.4% or approximately 3.3 million were marked by a ventral or adipose fin clip. The number of fingerlings stocked in Tustumena Lake ranged from 400,000 in 1978 to 17 million in 1984. The mean size of hatchery fingerlings at the time of release ranged from 25-30 mm in

Table 2. Summary of sockeye salmon eggs taken from Tustumena Lake, 1974-1991.

Brood year	Tributary			
	Glacier Flats	Seepage Creek	Bear Creek	Total eggs
1974	300,000	---	---	300,000
1975	5,857,000	---	---	5,857,000
1976	7,372,000	777,000	919,000	9,068,000
1977	4,931,000	---	864,000	5,795,000
1978	10,800,000	---	7,900,000	18,700,000
1979	3,600,000	---	3,500,000	7,100,000
1980	6,400,000	---	10,000,000	16,400,000
1981	10,200,000	---	10,200,000	20,400,000
1982	10,200,000	---	10,300,000	20,500,000
1983	10,200,000	---	10,200,000	20,400,000
1984	10,200,000	---	10,200,000	20,400,000
1985	14,500,000	---	9,200,000	23,700,000
1986	13,100,000	---	9,100,000	22,200,000
1987	13,441,000	---	7,572,000	21,013,000
1988	19,400,000	---	---	19,400,000
1989	16,470,000	---	---	16,470,000
1990	7,185,000	---	7,625,000	14,810,000
1991	---	---	17,700,000	17,700,000
Total	164,156,000	777,000	115,280,000	280,213,000
Mean	9,656,235		8,234,286	15,567,389

Table 3. Annual mean fecundity for sockeye salmon stocks used for enhancement at Tustumena Lake, 1975-1988.

Sample year	Stock	Mean fecundity
1975	Glacier Flats Creek	3,499
1976	Glacier Flats Creek	3,134
	Bear Creek	3,095
	Seepage Creek	3,291
1977	Glacier Flats Creek	3,710
1978	Glacier Flats Creek	3,523
	Bear Creek	3,502
1979	Glacier Flats Creek	3,522
	Bear Creek	3,503
1980	Glacier Flats Creek	N.A.
	Bear Creek	N.A.
1981	Glacier Flats Creek	3,233
	Bear Creek	3,071
1982	Glacier Flats Creek	3,246
	Bear Creek	3,123
1983	Glacier Flats Creek	3,530
	Bear Creek	3,226
1984	Glacier Flats Creek	3,164
	Bear Creek	2,994
1985	Glacier Flats Creek	3,203
	Bear Creek	3,045
1986	Glacier Flats Creek	3,000
	Bear Creek	2,991
1987	Glacier Flats Creek	3,246
	Bear Creek	3,026
1988 \a	Glacier Flats Creek	3,644
Overall means	Glacier Flats Creek	3,358
	Bear Creek	3,158
	All stocks combined	3,271

\a No fecundity measurements taken after 1988.

Table 4. Summary of sockeye salmon fingerlings released into Tustumena Lake from Crooked Creek Hatchery, 1976-1991.

	Glacier Flats Creek			Bear Creek			Total		
Release year	Number stocked	Number marked \a	Percent marked	Number stocked	Number marked \b	Percent marked	Number stocked	Number marked	Percent marked
1976	1,137,784	--	--	--	--	--	1,137,784	--	--
1977	--	--	--	--	--	--			
1978	400,000	--	--	--	--	--	400,000	--	--
1979	4,864,193	30,502	0.63	2,899,785	36,095	1.24	7,763,978	66,597	0.86
1980	2,706,610	32,669	1.20	2,499,232	32,758	1.31	5,205,842	65,427	1.26
1981	4,967,526	198,409	3.99	3,809,045	253,947	6.67	8,776,571	452,356	5.15
1982	8,299,560	210,114	2.53	7,648,602	248,639	3.25	15,948,162	458,753	2.88
1983	9,760,100	201,800	2.07	7,174,800	218,400	3.04	16,934,900	420,200	2.48
1984	9,750,000	202,400 \c	2.08	7,300,000	29,400	0.40	17,050,000	433,900	2.54
		202,100	2.07						
		404,500	4.15						
1985	9,587,804	37,800	0.39	6,805,423	137,111 \c	2.01	16,393,227	300,227	1.83
					135,312	1.99			
					272,432	4.00			
1986	5,490,162	101,162	1.84	8,071,821	123,821	1.53	13,561,983	224,983	1.66
1987	7,798,000	124,000	1.59	7,404,000	106,000	1.43	15,202,000	230,000	1.51
1988	3,225,000	90,400	2.80	3,047,000	90,000	2.95	6,272,000	180,400	2.88
1989	6,005,000	90,000	1.50	--	--	--	6,005,000	182,000	3.03
		92,000 \b	1.53						
1990	6,013,500	163,500	2.72	--	--	--	6,013,500	163,500	2.72
1991	6,000,000	80,000	1.33	--	--	--	6,000,000	155,000	2.58
		75,000 \b	1.25						
		155,000	2.58						
Total	86,005,239	1,931,856	1.85	56,659,708	1,411,483	2.35	142,664,947	3,333,343	2.41

\a Right ventral clip, unless noted otherwise.
\b Left ventral clip, unless noted otherwise
\c Adipose clip.

length and 0.13-0.23 g in weight, while wild fingerlings sampled in the lake near the release sites at the time of stocking ranged in size from 26-28 mm and 0.10-0.24 g (Table 5).

The summary of catches and mean sizes (weights) of emergent sockeye salmon fry migrating into Tustumena Lake from Bear and Glacier Flats Creeks in 1988 is presented in Table 6. Catch-per-unit-effort (CPUE) i.e., the catch-per-hour, ranged from 42-6,820 at Bear Creek and 8-55 at Glacier Flats Creek. Migrating emergent fry at Glacier Flats Creek were not sampled as frequently as at Bear Creek; however, considering similar parent-year escapements at both creeks in 1987, the relatively low CPUE for emergent fry at Glacier Flats Creek during the sampling period suggests a lower fry survival, and/or an earlier migration timing. Mean weights of emergent sockeye salmon fry migrating from Bear Creek in 1988 ranged between 0.13-0.16 g. Smaller-sized fry were caught after 31 May at Bear Creek, possibly a result of a later spawning group of adults. The mean size of emergent fry sampled at Glacier Flats Creek were larger than fry at Bear Creek as their mean weight ranged from 0.15-0.20 g.

Finally, during the 1988 emergent fry sampling, the timing of peak migration (CPUE) in both creeks appeared to be similar. The peak CPUE occurred about 10 May for both creeks, and a second smaller peak occurred about 25 May for fry migrating from Bear Creek (Figure 2). The peak migration for fry in Bear Creek coincided with a dramatic increase in creek temperature from about 4° C to 7° C (Figure 2A). Water temperature ranged from 0-7° C in Bear Creek during the sampling period. At Glacier Flats Creek the water temperature fluctuated less (3-6° C) than in Bear Creek (Figure 2B), and although peak fry migration occurred as the temperature was increasing, it did not occur when the water temperature was the highest.

Table 5. Comparison of the mean size of hatchery-reared sockeye salmon fingerlings at time of release with wild fingerlings collected in Tustumena Lake for brood years 1979-1990.

Brood year	Release date	Stock	Weight (g)	Fork length (mm)
1979	12-13 Jun 1980	Bear Creek	0.22	29
		Glacier Flats	0.22	29
		Wild	0.14	28
1980	16-18 Jun 1981	Bear Creek	0.21	29
		Glacier Flats	0.21	29
		Wild	0.15	28
1981	14-18 Jun 1982	Bear Creek	0.21	28
		Glacier Flats	0.21	28
		Wild	--	--
1982	13-17 Jun 1983	Bear Creek	0.22	29
		Glacier Flats	0.21	28
		Wild	0.16	27
1983	18-21 Jun 1984	Bear Creek	0.22	29
		Glacier Flats	0.23	30
		Wild	0.16	27
1984	17-18 Jun 1985	Bear Creek	0.13	26
		Glacier Flats	0.13	25
		Wild	0.24	28
1985	24-25 Jun 1986	Bear Creek	0.20	--
		Glacier Flats	0.21	--
		Wild	0.10	28
1986	16-17 Jun 1987	Bear Creek	0.19	27
		Glacier Flats	0.16	27
		Wild	0.14	26
1987	22 Jun 1988	Bear Creek	0.28	--
		Glacier Flats	0.23	--
		Wild	0.16	--
1988	19 June 1989	Glacier Flats	0.21	27
		Wild	0.15	29
1989	13 June 1990	Glacier Flats	0.23	--
		Wild	0.09	27
1990	18-20 Jun 1991	Glacier Flats	0.23	--
		Wild	0.12	26

Table 6. Summary of catches and mean sizes of emergent sockeye salmon fry migrating into Tustumena Lake from Bear and Glacier Flats Creeks, 1988.

Sample year	Sample period	Sample location	Number fry caught	CPUE	Mean fry weight (g)
13 Apr	2000-0800	Bear Creek	502	42	0.15
19 Apr	2000-0800	Bear Creek	1,619	135	0.15
27 Apr	2000-0800	Bear Creek	1,526	127	0.15
28 Apr	2000-0800	Bear Creek	2,118	177	0.15
03 May	2000-0800	Bear Creek	1,063	89	0.15
04 May	2100-0200	Bear Creek	1,237	103	0.14
10 May	2100-2030	Bear Creek	63	126	0.15
	2130-2230		732	732	
	0000-1000		6,820	6,820	
		Total	7,615	3,046	
16 May	2100-0200	Bear Creek	2,314	463	0.16
23 May	2100-0200	Bear Creek	9,206	1,650	0.13
31 May	2030-0300	Bear Creek	10,712	1,648	0.14
08 Jun	2000-0800	Bear Creek	5,200	433	0.14
15 Jun	2100-0800	Bear Creek	299	27	0.14
20 Apr	2000-0800	Glacier Flats	142	12	0.15
09 May	2000-0800	Glacier Flats	655	55	0.17
17 May	2100-0700	Glacier Flats	114	11	0.20
24 May	2100-0700	Glacier Flats	72	8	0.16

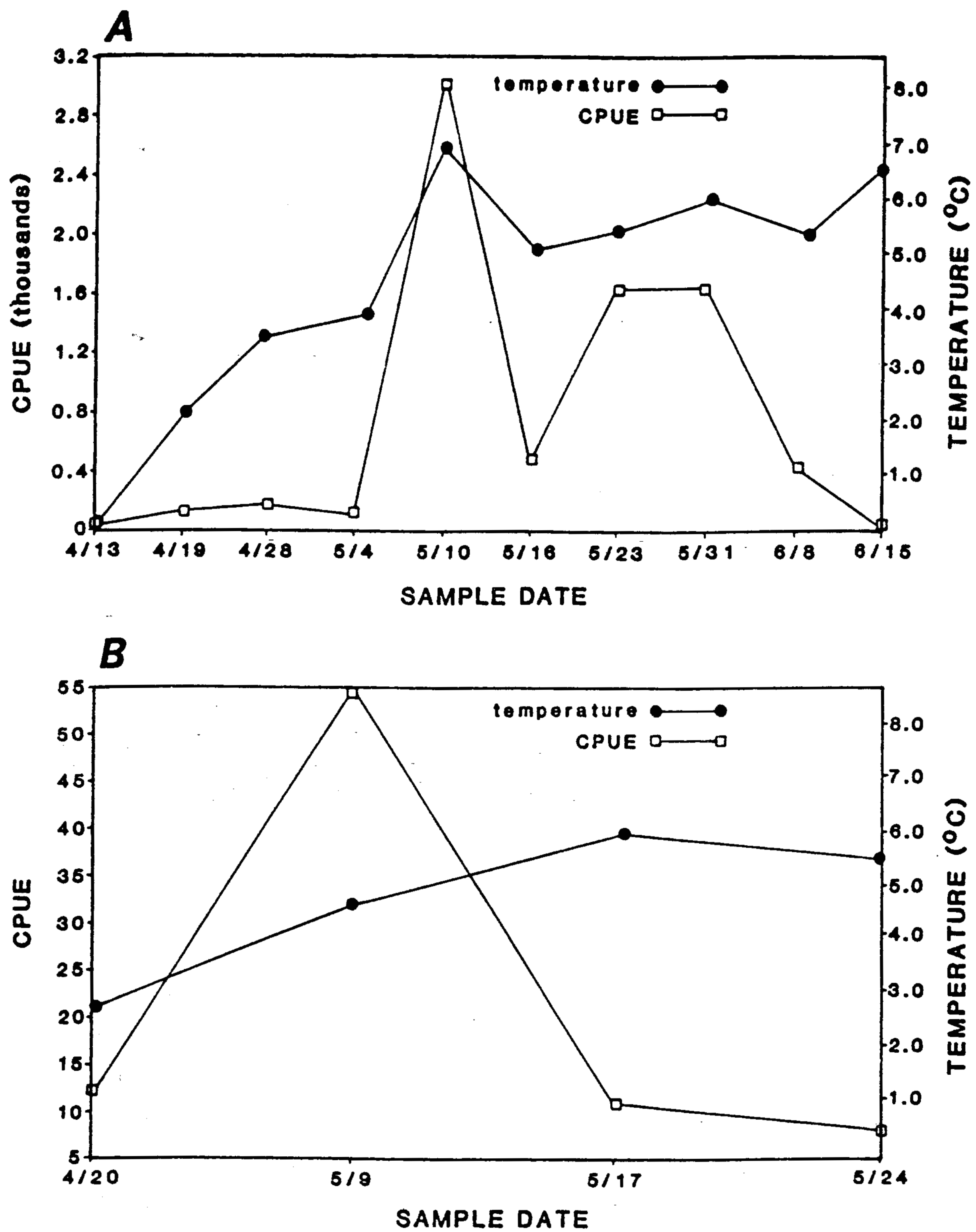


Figure 2. Migration timing of emergent sockeye salmon fry entering Tustumena Lake from Bear Creek (A) and Glacial Flats Creek (B), 1988.

Juvenile Sockeye Salmon Population Estimates and Distributions, Sizes, and Age Structure-- Limnetic population estimates of juvenile sockeye salmon rearing in Tustumena Lake based on hydroacoustic/townet surveys during 1981-1991 are summarized in Table 7. Total population estimates of juvenile sockeye salmon during the early season surveys (June-early July) ranged between 15-25 million, during the middle season surveys (late July-mid August) between 9-46 million, and during the late season surveys (September) between 7-28 million. In some years, the fall estimate was nearly as large as an earlier survey, and in 1987, the population estimate in the fall survey was larger than the July survey, indicating incomplete recruitment of juveniles to the limnetic area of the lake by July. The population estimate of age-0 juvenile sockeye salmon for all surveys ranged between 6-42 million and for age-1 from <1 to 13 million. Since 1986, the population estimate of juvenile sockeye in the fall (September) has been relatively consistent, ranging from 13.2 to 18.4 million.

The horizontal distribution (percent relative density by transect) of juvenile sockeye salmon for the late June-early July surveys of 1981-1983 indicate an increasing number of fish from transects 1 to 8 (Figure 3), or from the upper to lower part of Tustumena Lake (Figure 1). Overall, the relative fish density as a percentage of the total for the late June-early July surveys ranged from an average of 2% at transect 1 to 26% at transect 7. During the late July-mid August surveys of 1981-1987, juvenile sockeye salmon appeared more dispersed throughout the lake (Figure 4). The relative fish density as a percentage for these surveys ranged from an average of 5% at transect 8 to 16% at transect 5. Excluding transect 8, the relative fish density as a percentage was relatively equal among the transects, averaging between 12-16%, with the greatest average densities at transects 4 and 5 near limnological Station B (Figure 1). Finally, during the September surveys, relative fish densities by transect indicated a wide dispersion of fish throughout the lake (Figure 5). Relative fish densities for these surveys ranged from an average of 9% at transect 8 to 17%

Table 7. Summary of hydroacoustic surveys and juvenile sockeye salmon population estimates in Tustumena Lake during 1981-1991.

Survey year	Survey date	Juvenile sockeye population estimates (millions)					
		Age-0	C.I. \a	Age-1	C.I. \a	Total	C.I. \a
1981	02-05 Jun	--	--	--	--	14.7	1.97
	28 Jun-01 Jul	--	--	--	--	25.0	6.82
	21-23 Sep	6.3	--	0.45	--	6.8	--
1982	28 Jun-04 Jul	10.6	3.04	4.9	1.27	15.5	3.92
	26-29 Jul	17.0	--	2.2	--	19.2	--
	27 Sep-01 Oct	10.0	--	1.1	--	11.1	--
1983	08-11 Jul	23.6	--	1.4	--	25.0	--
	10-16 Aug	22.0	8.10	2.4	1.30	24.4	10.00
	26-29 Sep	20.8	7.00	3.9	2.60	24.7	8.40
1984	30 Jul-03 Aug	26.9	--	3.4	--	30.3	--
	25-27 Sep	19.4	8.00	3.9	2.00	23.3	6.77
1985	24 Jul-06 Aug	42.0	14.40	4.2	1.50	46.2	15.90
	20 Sep-03 Oct	23.8	8.50	4.5	2.00	28.3	12.50
1986	24 Jul-03 Aug	14.6	4.40	13.0	4.00	27.6	8.40
	22-24 Sep	9.6	1.70	6.9	1.30	16.5	3.00
1987	27-28 Jul	6.5	--	2.3	--	8.8	4.30
	28 Sep-01 Oct	9.8	--	3.4	--	13.2	1.60
1988	22-25 Sep	11.6	2.10	3.5	0.70	15.1	2.80
1989	13-14 Sep	12.0	--	4.6	--	16.6	--
1990	25-27 Sep	14.7	--	3.7	--	18.4	--
1991	25-Sep	12.4	--	2.9	--	15.3	--

\a +/-95% confidence interval.

-- Population estimates of these age classes and/or these confidence intervals have not been finalized.

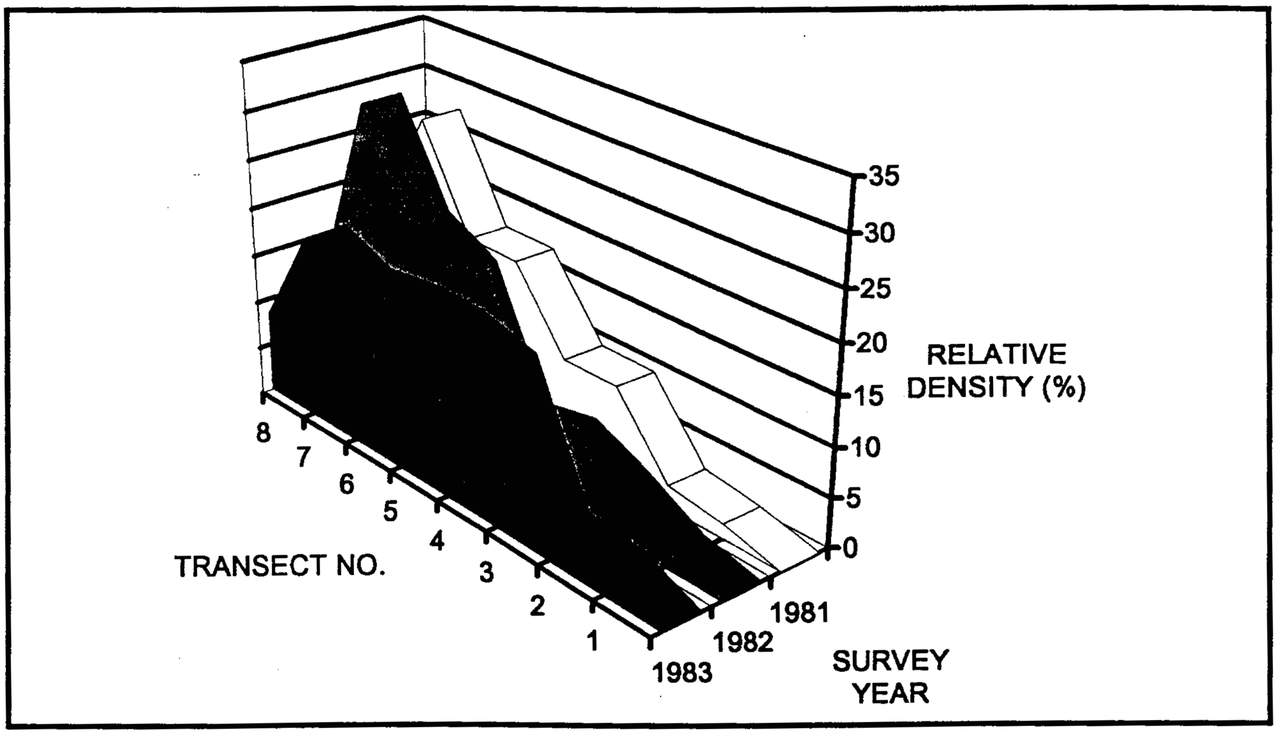


Figure 3. Relative density of juvenile sockeye salmon by transect for 1981-1983 hydroacoustic surveys conducted during late June-early July in Tustumena Lake.

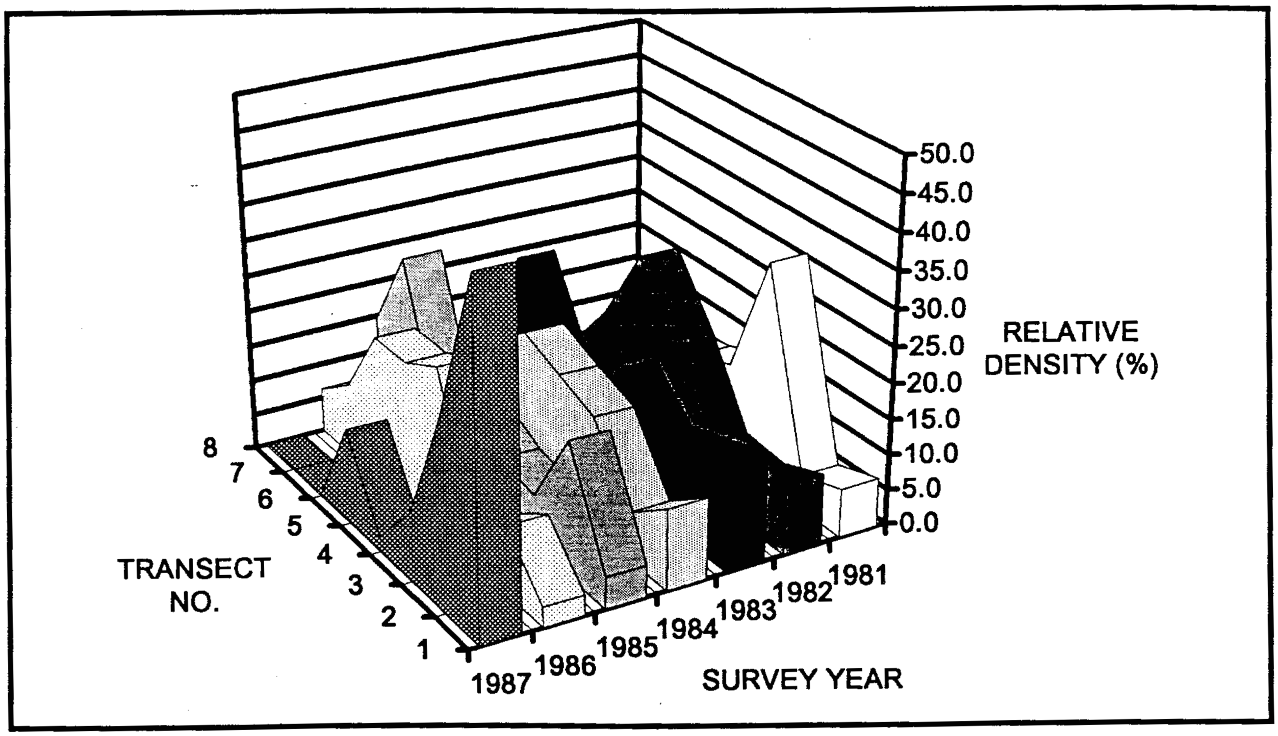


Figure 4. Relative density of juvenile sockeye salmon by transect for 1981-1987 hydroacoustic surveys conducted during late July-August in Tustumena Lake.

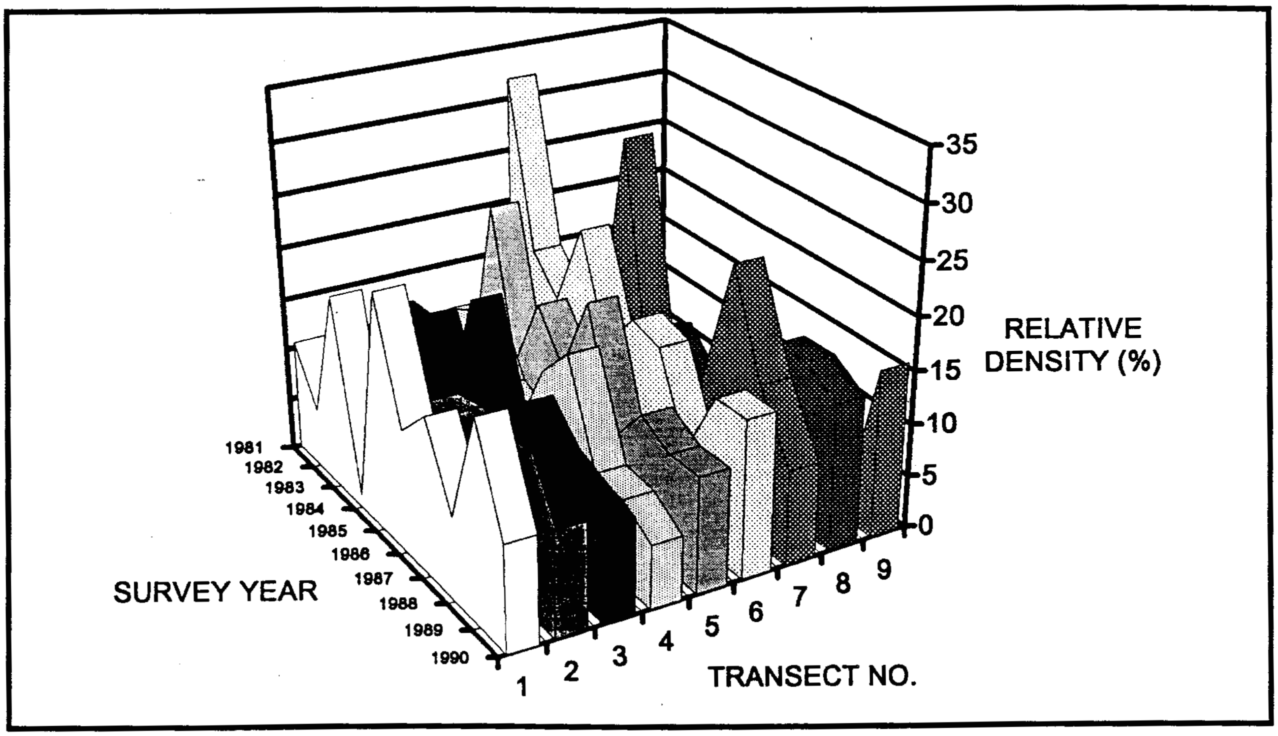


Figure 5. Relative density of juvenile sockeye salmon by transect for 1981-1990 hydroacoustic surveys conducted during September in Tustumena Lake.

at transect 6. Similar to the late July-mid August surveys, higher average fish densities were found at transects 5 and 6 (near Station B), and at transect 7.

Comparison of the vertical distribution of juvenile sockeye salmon (percent relative density by depth interval) for the July and September surveys (1983-1990) indicated a deeper distribution of fish during September (Figure 6). During the July surveys, the vertical distribution was quite consistent each year (Figure 6A), with >70% of the fish density near the surface in the 2.5-5 m depth interval. Relative fish densities in the 2.5-5 m depth interval during the September surveys ranged between 25-50% (Figure 6B). The decrease in the percentage of fish in the upper depth interval during the September surveys suggests that juvenile sockeye salmon are distributed deeper during a shorter photoperiod. This was further supported by the results of replicated runs of a transect during the day and night in September of 1981 when larger concentrations of fish were found near the surface during the day (Thorne and Thomas 1981). This diel distribution pattern is atypical for sockeye salmon (Narver 1970; Eggers 1978; Levy 1987; Kyle 1988b) and may be the affect of limited light on the feeding behavior of sockeye salmon in glacial lakes.

The mean sizes of age-0 sockeye salmon fingerlings captured by townet during the September surveys (1980-1991) ranged between 50-61 mm and 1.3-2.5 g, and averaged 56 mm and 1.9 g (Table 8). Age-1 fingerling sockeye salmon ranged in size between 73-80 mm and 4.1-5.8 g, and averaged 76 mm and 4.8 g. The coefficients of variation for the mean sizes of juvenile sockeye salmon rearing in Tustumena Lake during the fall of 1980-1991 were less than 0.20. The total estimated biomass of juvenile sockeye salmon rearing in Tustumena Lake during the fall of 1981-1991 ranged between 12,000-75,000 kg and averaged 43,950 kg (Table 9). Of the total mean fingerling biomass, 27,200 kg (62% of the total) and 16,750 kg (38% of the total) comprised of age-0 and age-1 fingerlings, respectively.

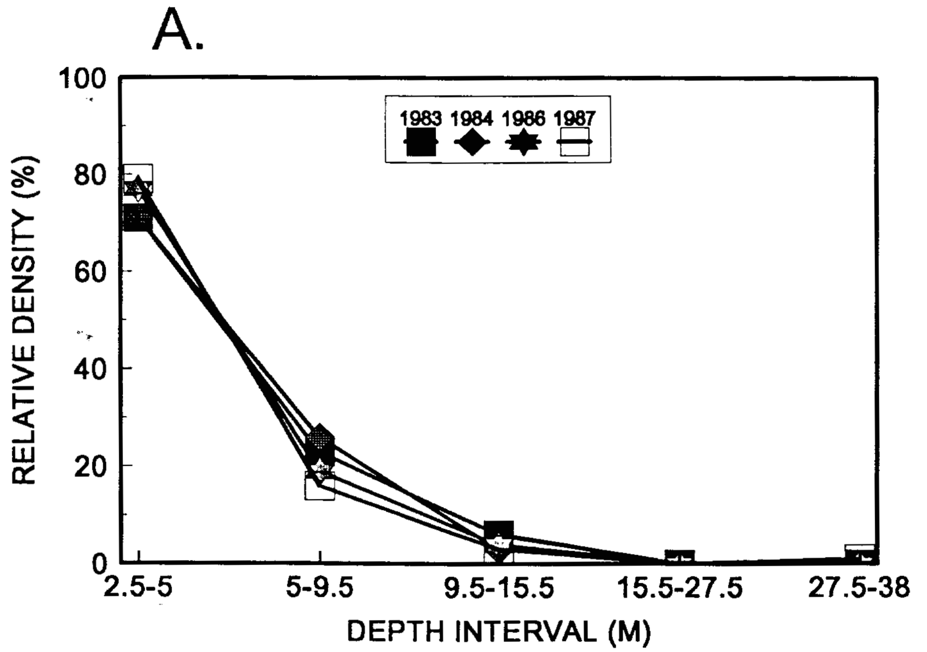


Figure 6. Relative density of juvenile sockeye salmon by depth interval for 1983-1990 hydroacoustic surveys conducted during July (A) and September (B) in Tustumena Lake.

Table 8. Mean sizes of juvenile sockeye salmon (age-0 and age-1) rearing in Tustumena Lake during September, 1980-1991.

Sample date	Age-0					Age-1				
	Mean length (mm)	S.D.	Mean weight (g)	S.D.	Sample size	Mean length (mm)	S.D.	Mean weight (g)	S.D.	Sample size
22 Sep 1980	59	6.6	2.3	0.7	222	80	3.5	5.7	0.7	20
19-23 Sep 1981	55	5.1	1.6	0.4	197	73	4.6	3.8	0.7	21
27 Sep-01 Oct 1982	54	5.1	1.8	0.5	194	74	3.9	4.6	0.9	17
26 Sep-06 Oct 1983	60	6.1	2.5	0.7	562	80	5.0	5.8	1.1	55
18 Sep-04 Oct 1984	61	4.6	2.5	0.6	388	79	3.7	5.3	0.8	186
18 Sep-03 Oct 1985	56	5.6	2.1	0.6	173	78	5.0	5.6	1.2	52
22-25 Sep 1986	50	6.4	1.3	0.5	156	73	4.5	4.1	0.7	92
28 Sep-01 Oct 1987	53	5.9	1.8	0.6	143	71	3.8	4.2	0.6	50
22-25 Sep 1988	55	5.3	1.8	0.5	303	75	3.6	4.5	0.6	89
13-14 Sep 1989	52	5.7	1.9	0.6	47	74	4.6	5.1	0.9	18
25-27 Sep 1990	57	5.5	1.5	0.4	200	75	2.9	3.4	0.5	50
25 Sep 1991	57	5.4	2.0	0.5	202	78	6.5	5.1	1.2	47
Mean	56		1.9			76		4.8		
Coefficient of variation	0.05		0.19			0.04		0.16		

Table 9. Estimated biomass of juvenile (age-0 and age-1) sockeye salmon rearing in Tustumena Lake during September, 1981-1991.

	Age-0			Age-1			Total
Rearing year	Estimated number (millions)	Mean weight (g)	Estimated biomass (kg)	Estimated number (millions)	Mean weight (g)	Estimated biomass (kg)	estimated juvenile biomass (kg)
1981	6.3	1.6	10,080	0.5	3.8	1,710	11,790
1982	10.0	1.8	18,000	1.1	4.6	4,876	22,876
1983	20.8	2.5	52,000	3.9	5.8	22,620	74,620
1984	19.4	2.5	48,500	3.9	5.3	20,670	69,170
1985	23.8	2.1	49,980	4.5	5.6	25,200	75,180
1986	9.6	1.3	12,480	6.9	4.1	28,290	40,770
1987	9.8	1.8	17,640	3.4	4.2	14,280	31,920
1988	11.6	1.8	20,880	3.5	4.5	15,750	36,630
1989	12.0	1.9	22,800	4.6	5.1	23,460	46,260
1990	14.7	1.5	22,050	3.7	3.4	12,580	34,630
1991	12.4	2.0	24,800	2.9	5.1	14,790	39,590
Mean	13.7	1.9	27,201	3.5	4.7	16,748	43,949

Smolt Outmigration Estimates, Sizes, Age Structure, Hatchery Contribution, and Hatchery Fingerling-to-Smolt Survival-- The initiation of the sockeye salmon smolt migration (>1,000 smolts/day) and the 50% midpoint of the migration varied by two weeks or less during 1981-1991 (Table 10). The earliest date of initiation of smolting was 13 May 1981, and the earliest midpoint of the migration was 28 May 1984. The latest date of initiation of migration was 26 May 1983, and the latest midpoint of the migration was 15 June 1985. The mean date of the midpoint of the smolt migration during 1981-1991 was 08 June.

The estimated number of sockeye salmon smolts migrating from Tustumena Lake during 1981-1991 varied from a low of 2.3 million to as high as 16.6 million, and averaged 7.4 million (Table 11). Of the 7.4 million average number of sockeye salmon smolts produced, 5.0 million (68%) and 2.4 million (32%) comprised of age-1 and age-2 smolts, respectively. During 1981-1986, the age composition of age-1 smolts was relatively consistent (70-84%); however, since 1987 the composition of age-1 smolts averaged 47%. The overall (1981-1991) smolt age composition was 63% age-1 and 37% age-2.

The mean size of neither age-1 or age-2 smolts fluctuated substantially during 1980-1991 as the coefficients of variation for annual mean lengths and weights ranged from 0.03-0.12 (Table 12). Age-1 smolts ranged in mean length between 64-73 mm and in weight from 2.2-3.3 g, while age-2 smolts ranged in size between 77-88 mm and 3.4-5.2 g. The overall mean size of age-1 smolts was 69 mm and 2.7 g, and for the age-2 smolts was 82 mm and 4.4 g. The smallest age-1 and age-2 smolts were observed in 1987; however, after 1987, smolt sizes were comparable to previous years.

The annual total sockeye smolt biomass averaged 24,365 kg and ranged between 7,284-52,506 kg during 1981-1991 (Table 13). Of the mean total smolt biomass produced, 13,974 kg (57% of the total) and 10,391 kg (43% of the total)

Table 10. Timing of the Kasilof River sockeye salmon smolt migration, 1981-1991.

Smolt year	Starting date \a	50% midpoint	Ending date \b
1981	13 May	30 May	01 Jul
1982	24 May	13 Jun	14 Jul
1983	26 May	13 Jun	05 Jul
1984	16 May	28 May	10 Jul
1985	24 May	15 Jun	17 Jul
1986	21 May	13 Jun	17 Jul
1987	14 May	12 Jun	11 Jul
1988	11 May	09 Jun	08 Jul
1989	14 May	04 Jun	30 Jun
1990	19 May	06 Jun	29 Jun
1991	21 May	08 Jun	08 Jul
Mean	18 May	08 Jun	08 Jul

\a First day trap catch reached 1,000 smolts.

\b Date traps were removed from river.

Table 11. Estimated number and percentage of age-1 and age-2 sockeye salmon smolts migrating from Tustumena Lake, 1981-1991.

Smolt year	Age-1 smolts (millions)	C.I. \a (millions)	Age-1 composition	Age-2 smolts (millions)	C.I. (millions)	Age-2 composition	Age-1 and age-2 smolts (millions)	C.I. (millions)
1981	1.865	--	82%	0.401	--	18%	2.266	0.31
1982	4.140	0.96	80%	1.010	0.23	20%	5.150	0.69
1983	6.817	0.73	84%	1.328	0.13	16%	8.145	1.37
1984	11.390	1.95	80%	2.869	1.00	20%	14.259	1.67
1985	12.580	0.56	76%	4.001	0.56	24%	16.581	1.89
1986	5.268	0.38	70%	2.223	0.37	30%	7.491	2.08
1987	1.074	0.07	23%	3.540	0.07	77%	4.614	1.16
1988	2.056	0.10	45%	2.549	0.10	55%	4.605	1.03
1989	3.109	0.16	51%	3.009	0.16	49%	6.118	1.30
1990	3.961	0.24	53%	3.521	0.24	47%	7.482	1.87
1991	2.400	0.12	51%	2.335	0.12	49%	4.735	0.92
Mean	4.969		63%	2.435		37%	7.404	

\a +/-95% confidence interval.

Table 12. Summary of the weighted mean size of sockeye salmon smolts migrating from Tustumena Lake, 1980-1991.

	Age-1					Age-2				
Smolt year	Sample size	Mean length (mm)	S.D.	Mean weight (g)	S.D.	Sample size	Mean length (mm)	S.D.	Mean weight (g)	S.D.
1980	846	68	4.3	2.7	0.5	122	86	4.9	4.7	1.5
1981	791	70	4.4	2.8	0.5	153	88	4.6	5.1	0.8
1982	566	69	3.7	2.9	0.6	148	82	4.2	4.8	0.7
1983	712	70	3.8	2.9	0.5	451	83	5.4	5.0	0.9
1984	1,005	73	3.5	3.3	0.6	187	85	4.4	5.2	0.8
1985	981	70	2.8	2.6	0.5	282	84	5.4	4.3	0.7
1986	983	69	3.9	2.6	0.5	365	84	5.1	4.6	0.9
1987	412	64	6.1	2.2	0.6	1,223	77	4.8	3.4	0.6
1988	623	68	4.0	2.5	0.5	652	78	4.5	3.6	0.7
1989	609	66	4.4	2.7	0.5	516	81	4.5	4.1	0.7
1990	683	69	4.4	2.6	0.5	467	82	4.2	4.4	0.7
1991	529	68	3.5	2.6	0.4	489	80	3.2	4.0	0.5
Mean		69		2.7			82		4.4	
Coefficient of variation		0.03		0.09			0.04		0.12	

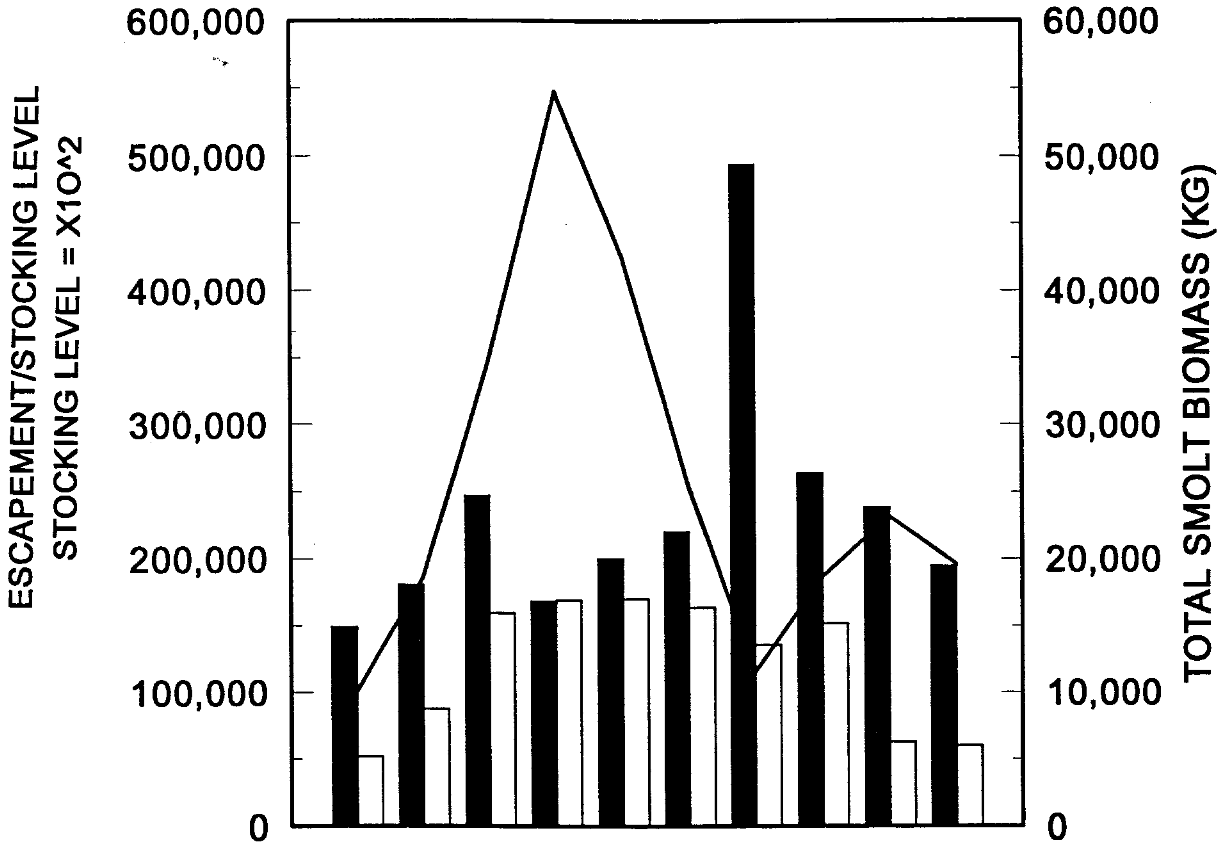
Table 13. Estimated biomass for age-1 and age-2 sockeye salmon smolts migrating from Tustumena Lake, 1981-1991.

Smolt year	Mean weight (g)		Estimated number of smolts (x 1000)		Estimated smolt biomass (kg)		Total estimated smolt biomass (kg)
	Age-1	Age-2	Age-1	Age-2	Age-1	Age-2	
1981	2.8	5.1	1,865	401	5,222	2,045	7,267
1982	2.9	4.8	4,140	1,010	12,006	4,848	16,854
1983	2.9	5.0	6,817	1,328	19,769	6,640	26,409
1984	3.3	5.2	11,390	2,869	37,587	14,919	52,506
1985	2.6	4.3	12,580	4,001	32,708	17,204	49,912
1986	2.6	4.6	5,378	2,123	13,983	9,766	23,749
1987	2.2	3.4	1,074	3,540	2,363	12,036	14,399
1988	2.5	3.6	2,056	2,549	5,140	9,176	14,316
1989	2.7	4.5	3,109	3,009	8,394	13,541	21,935
1990	2.6	4.2	3,961	3,521	10,299	14,788	25,087
1991	2.6	4.0	2,400	2,335	6,240	9,340	15,580
				Mean	13,974	10,391	24,365

comprised of age-1 and age-2 smolts, respectively. The broodyear with the highest smolt biomass occurred during the period of high stocking (~16 million), but from a lower escapement compared to broodyears before and after the broodyear with the highest smolt biomass when stocking levels were similar (Figure 7). That is, the highest (54,800 kg) smolt biomass from natural production and stocking occurred from broodyear 1982, when the escapement was 169,000 and the stocking level was 16.9 million. In 1981 and 1983, the respective escapements were 247,000 and 200,400, the stocking levels were 15.9 million and 17.0 million, and smolt biomass was 34,700 kg and 42,500 kg. Thus, this suggests smolt biomass production is not primarily dependent upon escapement and stocking levels.

Moreover, there was not a significant ($p > .05$) relationship between parent escapements and total wild smolt biomass (Figure 8A), but there was a significant ($r^2 = .59$; $p = .009$) relationship between parent escapements and the percentage of wild pre-smolts that heldover in the lake for an additional year of rearing (Figure 8B). This latter relationship was significant ($r^2 = 0.56$; $p = .012$) even without the outlier point of the large 1985 escapement (~500,000). Thus, these relationships suggest that there is not a primary density-dependent response in smolt biomass produced from respective escapements, but there is a density-dependent response in the percentage of pre-smolts rearing an additional year.

From the 1984 release of 202,000 Glacier Flats Creek sockeye salmon fingerlings marked with a right ventral (RV) fin clip and 202,400 marked with an adipose (AD) fin clip (Table 4), a total of 140 RV and 230 AD fin-clipped age-1 smolts were recovered in 1985 (Table 14). This resulted in a 37.8% survival advantage for the control group (AD), or a differential mark mortality factor (DMF) of 1.64. In 1985 from the release of 135,312 Bear Creek fingerlings marked with a left ventral (LV) fin clip and 137,111 marked with an AD fin clip (Table 4), a total of 130 LV and 190 AD fin-clipped age-1 smolts were recovered



BROODYEAR/ STOCKING YEAR	79/80	80/81	81/82	82/83	83/84	84/85	85/86	86/87	87/88	88/89
Escapement ■	149,155	181,124	246,925	168,668	200,368	220,544	493,769	264,011	238,761	194,613
Stocking level (x10^2) □	52,058	87,766	159,481	169,349	170,500	163,932	135,619	152,020	62,720	60,050
Total Smolt Biomass (kg) —	10,070	18,646	34,688	54,791	42,474	25,419	11,539	18,681	23,182	19,639

Figure 7. Relationship of escapement and stocking level on total smolt biomass produced for broodyears 1979-1988.

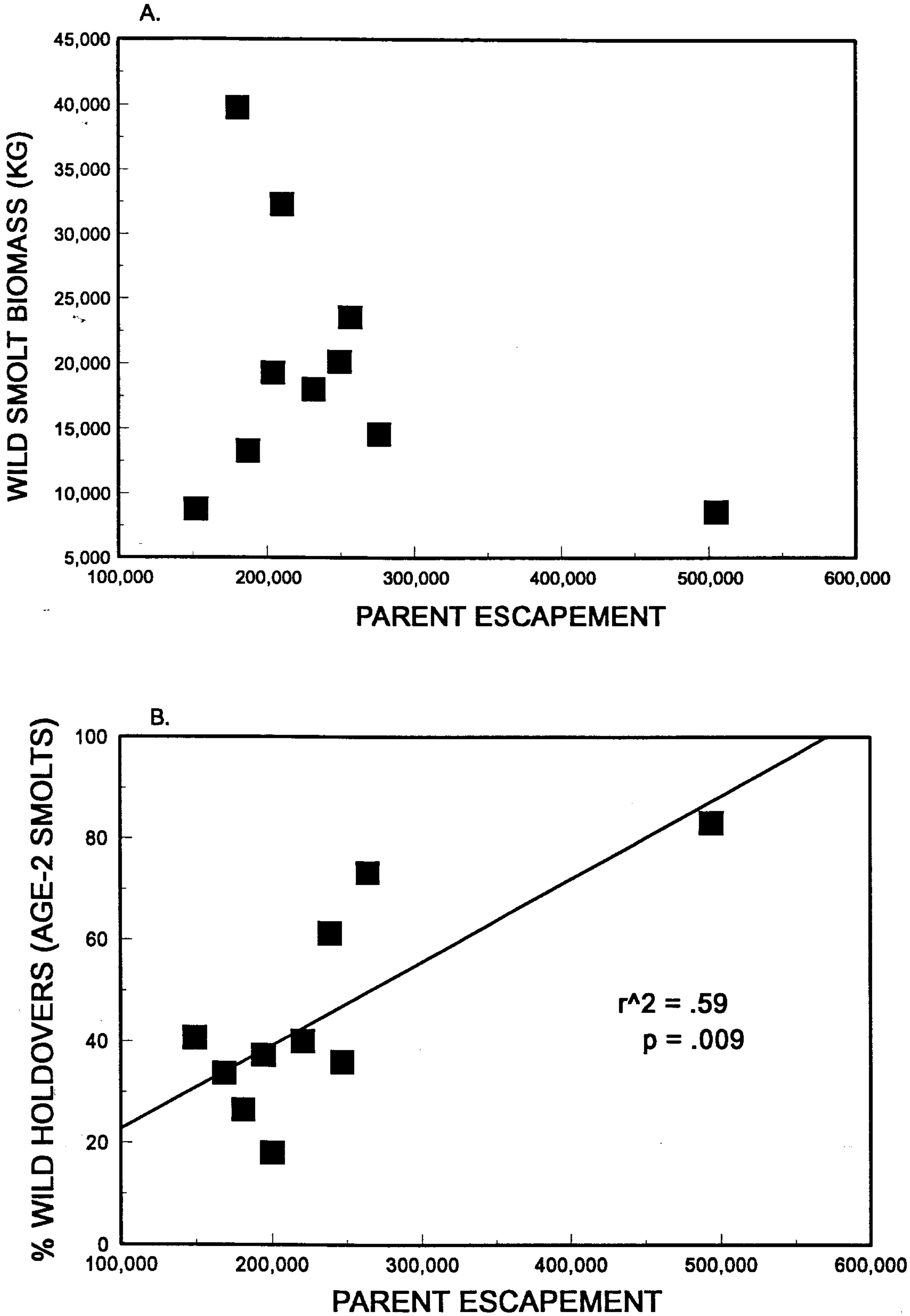


Figure 8. Relationship between parental escapement (minus fish used for egg-takes) and wild smolt biomass (A) and percentage of wild holdovers (B) for broodyears 1979-1988.

Table 14. The number of right ventral (RV) and adipose (AD) clipped age-1 sockeye salmon smolts (Glacier Flats Creek stock) recovered in 1985 and the differential mark mortality factor (DMF).

Sample period	Number AD clips recovered	Number RV clips recovered	DMF	Percent RV clips recovered	C.I. \a Percent RV Clips Lower (%)	Upper (%)
19-25 May	10	7		41.2	14.4	73.5
26 May-01 Jun	41	17		29.3	16.7	45.8
02-08 Jun	63	34		35.1	23.7	48.2
09-15 Jun	33	23		41.1	24.8	59.3
16-22 Jun	12	4		25.0	6.7	57.2
23-29 Jun	26	27		50.9	31.2	70.4
30 Jun-06 Jul	33	17		34.0	19.1	52.6
07-13 Jul	12	11		47.8	20.7	76.1
Overall	230	140	1.64	37.8	31.6	44.5

\a +/-95% confidence interval.

Table 15. The number of left ventral (LV) and adipose (AD) clipped age-1 sockeye salmon smolts (Bear Creek stock) recovered in 1986 and the differential mark mortality factor (DMF).

Sample period	Number AD clips recovered	Number LV clips recovered	DMF	Percent LV clips recovered	C.I. \a Percent LV Clips Lower (%)	Upper (%)
05-24 May	18	16		47.1	24.4	70.8
25-31 May	34	23		40.4	24.4	58.4
01-07 Jun	42	25		37.3	23.3	53.6
08-14 Jun	27	20		42.6	24.5	62.7
15-21 Jun	23	12		34.3	16.8	56.7
22-28 Jun	12	12		50.0	22.3	77.7
29 Jun-05 Jul	9	8		47.1	17.0	79.2
06-17 Jul	25	14		35.9	18.6	57.3
Overall	190	130	1.46	40.6	33.6	48.0

\a +/-95% confidence interval.

in 1986 (Table 15). For this group, a 40.6% survival advantage was observed for AD-clipped fish for a DMF of 1.46. Thus, the average DMF for both releases was 1.5 and was applied to the number of all hatchery marked smolts recovered to estimate the total number of hatchery-produced smolts.

Using the 1.5 DMF factor, the estimated total number of hatchery smolts migrating from Tustumena Lake ranged from a low of 440,000 to a high of 4.7 million, and averaged 1.8 million during 1981-1991 (Table 16). The estimated percentage of the number of hatchery smolts contributing to the total smolt migration ranged between 4-37%, and averaged 24% for this period. A mean of 1.5 million hatchery age-1 smolts (31%), and 310,000 age-2 smolts (12%) contributed to the total smolt migration.

The estimated smolt survival rate for hatchery-released sockeye salmon fingerlings by release year during 1980-1991 ranged between 2-26%, and averaged 15% (Table 17). Survival for age-1 smolts varied considerably (1-25%) and averaged 12%. For age-2 hatchery-produced smolts, survivals ranged between 0.4-7%, and averaged 3%. In addition, a non-significant ($p > .05$) relationship was found between the number of fingerlings released and hatchery smolt biomass (Figure 9A). The variability in this relationship can be illustrated by noting that stocking levels ranging between 6-17 million produced smolt biomass ranging between 1,000-15,000 kg. In addition, the variability in this relationship may be substantially attributed to the hatchery fry-release technique, as fry released by helicopter (ground release) survived at an average rate of 19%, while those air dropped from a fixed-wing airplane survived at a rate of 9% (Figure 9B). Finally, there was no significant ($p > .05$) relationship between the number of hatchery fingerlings released and the percentage of hatchery pre-smolts that heldover in the lake for an additional year of rearing (Figure 9C).

Table 16. Estimated hatchery contribution of released sockeye salmon fingerlings to the total annual smolt production in Tustumena Lake, 1981-1991.

	Hatchery smolt production					
	Age-1		Age-2		Total hatchery smolts	
Smolt year	Number (millions)	Hatchery contribution	Number (millions)	Hatchery contribution	Number (millions)	Hatchery contribution
1981	0.42	22.7%	0.02	4.3%	0.44	19.6%
1982	1.31	31.7%	0.02	2.4%	1.33	26.0%
1983	2.77	40.7%	0.31	23.2%	3.08	37.8%
1984	4.14	36.3%	0.59	20.6%	4.73	33.2%
1985	3.50	27.8%	0.31	7.7%	3.81	23.0%
1986	1.62	30.2%	0.23	11.1%	1.85	24.8%
1987	0.64	59.2%	1.10	31.1%	1.74	37.1%
1988	1.07	52.0%	0.43	17.0%	1.50	32.6%
1989	0.94	30.3%	0.31	10.2%	1.25	20.4%
1990	0.08	2.0%	0.11	3.0%	0.19	2.5%
1991	0.18	7.0%	0.03	1.0%	0.21	4.3%
Mean	1.52	30.9%	0.31	12.0%	1.83	23.8%

Table 17. Hatchery fingerling to smolt survival by release year for sockeye salmon stocked in Tustumena Lake, 1980-1991.

Release year	Number of hatchery fingerlings released (millions)	Number of hatchery age-1 smolts produced (millions)	Fingerling to age-1 smolt survival	Number of hatchery age-2 smolts produced (millions)	Fingerling to age-2 smolt survival	Total number of hatchery smolts produced (millions)	Total fingerling-to-smolt survival
1980	5.21	0.42	8.1%	0.02	0.4%	0.44	8.4%
1981	8.78	1.31	14.9%	0.31	3.5%	1.62	18.5%
1982	15.95	2.77	17.4%	0.59	3.7%	3.36	21.1%
1983	16.93	4.14	24.5%	0.31	1.8%	4.45	26.3%
1984	17.05	3.50	20.5%	0.23	1.3%	3.73	21.9%
1985	16.39	1.62	9.9%	1.10	6.7%	2.72	16.6%
1986	13.56	0.64	4.7%	0.43	3.2%	1.07	7.9%
1987	15.20	1.07	7.0%	0.31	2.0%	1.38	9.1%
1988	6.27	0.94	15.0%	0.11	1.8%	1.05	16.7%
1989	6.01	0.08	1.3%	0.03	0.5%	0.11	1.8%
1990	6.01	0.18	3.0%	--	--	--	--
1991	6.00	--	--	--	--	--	--
Mean	11.11	1.52	11.5%	0.34	2.5%	1.99	14.8%

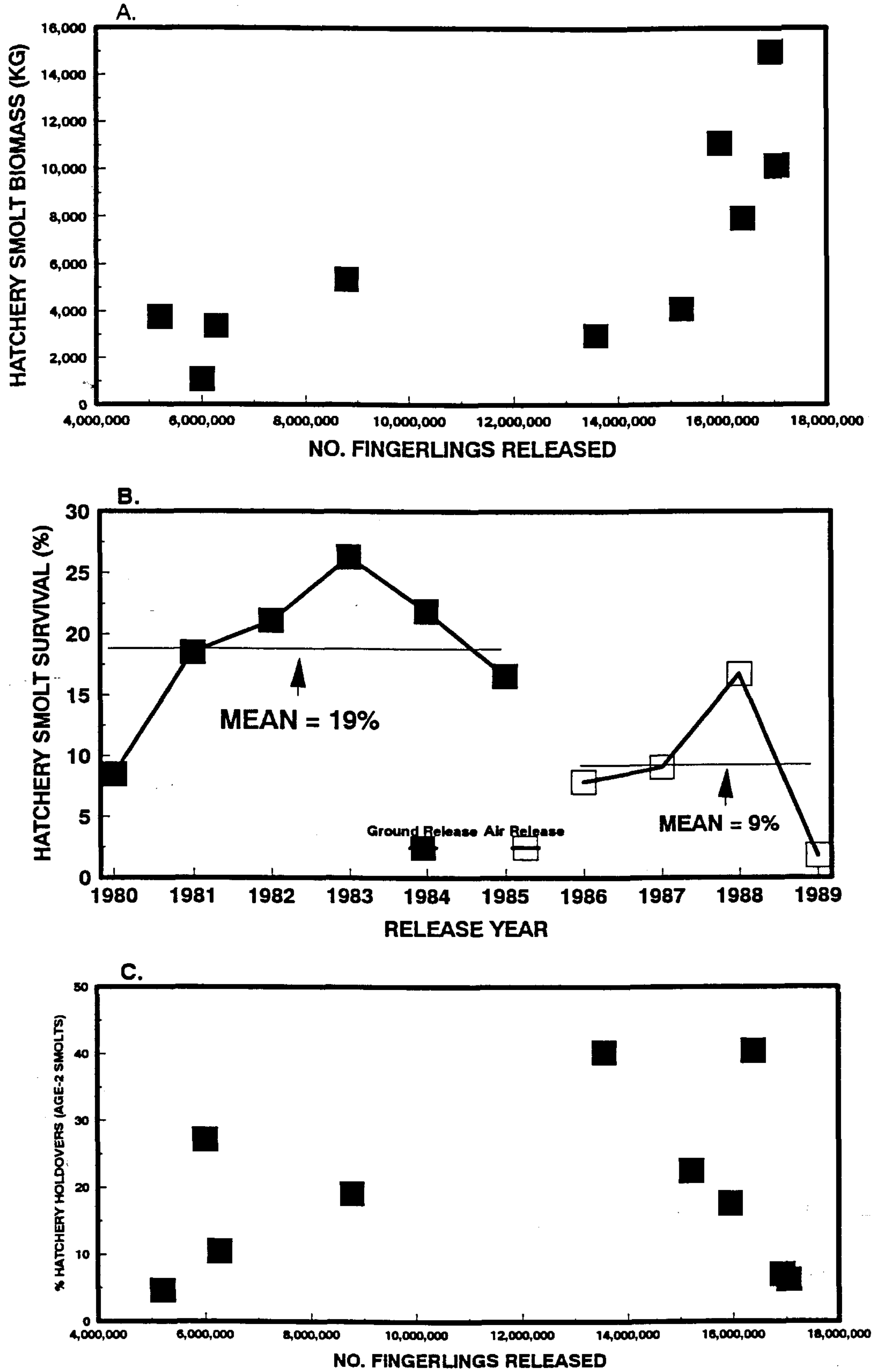


Figure 9. Relationship between hatchery smolt biomass and the number of fingerlings released for release years 1980-1989 (A), comparison of smolt survival for fry released by helicopter (ground release) and dropped from an airplane (air release) (B), and the relationship between the number of fingerlings released and the percentage of hatchery holdovers for release years 1980-1989 (C).

From the acoustically-derived population estimates of fall sockeye salmon fingerlings and estimates of smolts from trap catches, the percentages of fingerlings that survived and migrated as age-1 and age-2 smolts were derived (Table 18). During 1981-1984, the percentage of age-0 fingerlings that survived and migrated as age-1 smolts ranged between 55-68%. Since 1984, population estimates indicated that this percentage dropped and ranged between 11-33%. For release years 1986 and 1987, the percentage decreased and corresponded with a decrease in size of age-0 fingerlings (Table 9). The percentage of age-1 fingerlings that survived and migrated as age-2 smolts based on the two population estimates varied considerably during 1981-1986, and during half of these years was greater than 100%. This is believed to be a result of bias in the composition of age-1 fingerlings determined from townet samples, as the composition of age-2 smolts (sampled during the smolt migration) are approximately twice that for age-1 fall fingerlings in Tustumena Lake (Kyle 1988b). Thus, the bias in townet catches results in the underestimation of the composition of age-1 fingerlings, and therefore underestimates the number of age-1 fingerlings in the lake. Correspondingly, population estimates of age-0 fall fingerlings are overestimated by the biased townet-derived age compositions by assigning a greater percentage of the total population estimate to age-0 fingerlings.

Adult Returns and Age Structure-- Since 1968, sockeye spawning escapements (minus fish used for egg takes) have ranged between 38,000-494,000, and averaged 161,000 (Table 19). During 1979-1991(when total return information was available), escapements averaged 221,000, the commercial harvest averaged 673,000, and the total return averaged 921,000. The estimated harvest of sockeye salmon in the sport fishery and personal-use dipnet and gillnet fisheries during 1981-1991 averaged 21,000.

The smolt-to-adult survival for brood years with complete adult returns (1979-1985), ranged from 8-25%, and averaged 15% (Table 20). The greatest smolt-to-

Table 18. The percentage of fall fingerlings that migrated and survived as age-1 and age-2 smolts based on acoustical estimation of fall fingerlings and smolt trap estimates for Tustumena Lake, 1981-1991.

Rearing year	Estimated number of age-0 fingerlings (millions)	Estimated number of age-1 smolts (millions)	Estimated % of fingerlings that migrated and survived as age-1 smolts	Estimated number of age-1 fall fingerlngs (millionss)	Estimated nnumber of age-2 smolts (millions)	Estimated % of fingerlings that migrated and survived as age-2 smolts
1981	6.3	4.1	66%	0.5	1.3	296% \a
1982	10.0	6.8	68%	1.1	2.9	271%
1983	20.8	11.4	55%	3.9	4.0	103%
1984	19.4	12.6	65%	3.9	2.2	57%
1985	23.8	5.3	22%	4.5	3.5	79%
1986	9.6	1.1	11%	6.9	2.6	37%
1987	9.8	2.1	21%	3.4	3.0	88%
1988	11.6	3.1	27%	3.5	3.5	100%
1989	12.0	4.0	33%	4.6	2.3	50%
1990	14.7	2.4	16%	3.7	---	---
1991	12.4	---	---	2.9	---	---

\a See text.

Table 19. Summary of estimated escapements, harvests, and total returns of Tustumena Lake sockeye salmon, 1968-1991.

Return year	Sockeye sonar count \a	Number of sockeye used for egg take	Spawning escapement	Commercial harvest	Sport, dipnet, and personal-use harvest	Total return
1968	89,000	0	89,000	---	---	89,000
1969	46,000	0	46,000	---	---	46,000
1970	38,000	0	38,000	---	---	38,000
1971 \b	---	---	---	---	---	---
1972	113,000	0	113,000	---	---	113,000
1973	40,000	0	40,000	---	---	40,000
1974	70,000	205	69,795	---	---	70,000
1975	48,000	3,365	44,635	---	---	48,000
1976	139,000	5,463	133,537	---	---	139,000
1977	155,300	1,794	153,506	---	---	155,300
1978	116,600	6,681	109,919	---	---	116,600
1979	152,179	3,024	149,155	299,505	---	451,684
1980	187,154	6,030	181,124	619,231	---	806,385
1981	256,625	9,700	246,925	331,858	10,300	598,783
1982	180,239	11,571	168,668	1,066,816	9,786	1,256,841
1983	210,270	9,903	200,367	466,179	20,619	697,068
1984	231,685	11,141	220,544	524,377	28,908	784,970
1985	505,049	11,280	493,769	856,471	28,929	1,390,449
1986	275,963	11,952	264,011	1,602,827	50,450	1,929,240
1987	249,246 \c	10,485	238,761	853,200	38,697	1,141,143
1988	204,000	9,387	194,613	981,100	15,718	1,200,818
1989	158,206	7,367	150,839	401,000	14,560	573,766
1990	144,136	6,831	137,305	336,000	8,094	488,230
1991	238,269	8,850	229,419	405,900	9,132	653,301
Mean	167,301	7,502	161,430	672,651	21,381	920,975 \d

\a Includes counts or estimates from designated early period (prior to 15 June). Source: King and Tarbox (1991).

\b Sonar counters were inoperable.

\c The sonar count was less than the spawner survey count and because of an unusually early return of fish (before installation of sonar counter), the spawner survey counts and weir counts at Bear and Glacier Flats creeks were used as the system escapement.

\d 1979-1991 mean.

Table 20. Summary of estimated smolt-to-adult suvival for sockeye salmon in Tustumena Lake for brood years 1979-1987.

Brood year	Escapement	Total smolt production	Total adult production	Smolt-to-adult survival (%)
1979	149,155	2,875,000	708,000	24.6
1980	181,124	6,750,000	1,043,000	19.1
1981	246,925	11,060,000	1,911,000	19.7
1982	168,668	15,391,000	1,501,500	9.8
1983	200,368	14,803,000	1,139,000	7.7
1984	220,544	8,808,000	807,500	9.2
1985	493,769	3,623,000	553,500	15.3
1986	264,011	5,065,000	568,000	11.2 \a
1987	238,761	6,630,000	206,500	3.1 \b
Mean	240,369	8,333,889	937,600	15.1 \c

\a Excludes six-year-old adults that will not return until 1992.

\b Excludes five- and six-year-old adults that will not return until 1992 and 1993, respectively.

\c Mean for years of complete (all age classes) adult returns (1979-1985).

adult survival occurred from the 1979 broodyear escapement of 149,155 and a smolt production of 2.9 million, while the lowest occurred from the 1983 broodyear escapement of 200,368 and a corresponding smolt production of 14.8 million. Production of sockeye salmon in Tustumena Lake for broodyears 1979-1987 by life-stage is presented in the Appendix.

Finally, the percent composition of age-1.2 and age-1.3 sockeye salmon adults sampled from the Kasilof River fishwheels during 1969-1991 varied considerably, but the overall averages were equal (Table 21). That is, the composition of age-1.2 adults ranged between 6-59% and averaged 36.7%, while that for age-1.3 adults ranged between 7-69% and averaged 36.9%. The other two major age classes of adult sockeye salmon were age-2.2 and age-2.3, averaging 18% and 8% of the age composition, respectively during 1969-1991.

Tributary Spawner Counts, Distributions, and Adult Sampling-- Peak sockeye salmon spawner counts (and weir counts at Glacier Flats and Bear creeks) in the major tributaries of Tustumena Lake have varied over the years (Table 22). The three tributaries with the greatest variability (coefficients of variation) in these index counts over the years were Glacier Flats, Clear, and Seepage creeks. The mean spawner count for the major tributaries surveyed during 1975-1991 was 138,400. In addition, all except for two years (1975 and 1988), the tributary spawner counts of sockeye salmon were less than the reported sockeye salmon sonar counts.

Comparison of the relative percent distribution of spawners among the seven major tributaries before (1975-1983) and after (1984-1991) substantial returns of hatchery-produced fish (Table 23), reveals that spawner distributions drastically changed in only two. That is, the distribution of spawners in Glacier Flats Creek significantly ($p < .05$; Mann Whitney U-test) increased from 14% (16,600 fish) to 28% (50,700 fish) after hatchery returns. In contrast, non-enhanced sockeye salmon of Nikolai Creek decreased significantly ($p < .05$;

Table 21. Age class compositions of adult sockeye salmon collected by fishwheel from the Kasilof River, 1969-1991.

Return year	Sample size	Age class (%) 1.1	1.2	1.3	1.4	2.1	2.2	2.3	Other
1969	399		14.0	39.0	1.0		30.0	16.0	
1970	297	tr	32.0	37.0	2.0		16.0	11.0	1.0
1971	153		6.0	69.0			8.0	16.0	
1972	668	tr	42.0	36.0	1.0	tr	3.0	18.0	tr
1973	374		20.0	57.0			19.0	4.0	
1974	254		35.0	59.0		tr	4.0	2.0	
1975	931	1.0	29.0	7.0			58.0	4.0	1.0
1976	755	tr	32.0	20.0		tr	35.0	12.0	
1977	1,209	tr	30.0	30.0		1.0	28.0	11.0	
1978	967		42.0	35.0			14.0	9.0	
1979	590		52.2	37.2		tr	8.4	1.7	tr
1980	899		58.7	27.8			8.0	4.5	1.0
1981	1,479		30.2	62.2			6.0	1.6	
1982	1,518	1.0	34.0	49.5		0.1	10.7	4.7	0.1
1983	1,997		48.4	34.3			12.8	4.5	
1984	2,269		50.5	24.8	tr	0.2	17.9	6.6	
1985	3,063	0.2	57.3	21.8	0.1	0.1	17.8	2.6	
1986	1,660		40.9	42.0	0.3	0.8	11.9	4.6	0.2
1987	1,248		43.4	27.4		0.1	22.4	6.4	0.3
1988	2,282	0.9	37.5	32.9	0.1	0.1	18.6	10.6	0.2
1989	1,216	0.2	44.0	46.3	0.2		5.2	4.2	
1990	762	0.4	32.9	20.7	0.3		33.2	12.4	0.3
1991	2,106		31.5	33.4	0.1	0.1	29.0	5.8	0.3
Mean	1,178		36.7	36.9			18.1	7.5	

Source: King and Tarbox (1991).

Table 22. Peak sockeye salmon spawner counts in salmon-producing tributaries of Tustumena Lake, 1975-1991.

Return year	Nikolai	Crystal	Clear	Glacier Flats \a	Seepage	Moose	Bear \a	Total count
	Tributary							
1975	5,700	400	300	14,400	3,700	3,300	27,700	55,500
1976	12,000	800	300	7,100	800	14,000	51,800	86,800
1977	29,100	600	1,800	5,800	800	16,600	58,000	112,700
1978	34,200	200	200	4,700	1,100	15,900	43,400	99,700
1979	19,100	500	400	5,600	800	8,100	35,900	70,400
1980	10,000	1,000	2,100	15,500	1,800	15,600	125,000	171,000
1981	36,000	850	3,000	40,050	3,400	12,950	75,100	171,350
1982	16,800	1,800	4,200	17,350	1,650	13,400	51,350	106,550
1983	17,100	1,650	850	38,800	3,300	19,250	61,950	142,900
1984	8,250	150	2,600	76,200	6,250	14,000	54,350	161,800
1985	17,500	800	3,500	121,400	5,700	9,200	120,400	278,500
1986	11,900	1,400	2,700	60,600	2,000	21,200	102,900	202,700
1987	9,000	1,400	7,700	61,000	800	17,600	71,250	168,750
1988	10,850	600	5,800	40,000	1,400	17,750	127,550	203,950
1989	4,800	1,050	550	20,150	950	17,050	62,950	107,500
1990	7,450	900	200	14,350	1,200	18,800	46,300	89,200
1991	21,600	400	1,200	12,100	1,700	18,100	68,900	123,900
Mean	15,962	853	2,200	32,653	2,197	14,871	69,694	138,424
Coefficient of variation	0.58	0.55	0.95	0.94	0.75	0.30	0.43	

\a Weir counts and surveys; includes fish used for egg takes.

Table 23. Comparison of relative percent distribution of sockeye salmon among major tributaries of Tustumena Lake before (1975-1983) and after (1984-1991) substantial returns of hatchery-produced fish.

	Tributary						
Return year	Nikolai	Crystal	Clear	Glacier Flats	Seepage	Moose	Bear
1975	10.3	0.7	0.5	25.9	6.7	5.9	49.9
1976	13.8	0.9	0.3	8.2	0.9	16.2	59.8
1977	25.8	0.5	1.6	5.1	0.7	14.7	51.5
1978	34.3	0.2	0.2	4.7	1.1	15.9	43.5
1979	27.1	0.7	0.6	7.9	1.1	11.5	51.0
1980	5.8	0.6	1.2	9.0	1.1	9.1	73.1
1981	21.0	0.5	1.8	23.4	2.0	7.6	43.8
1982	15.8	1.7	3.9	16.3	1.5	12.6	48.2
1983	12.0	1.2	6.0	27.1	2.3	13.5	43.4
Mean	18.4	0.8	1.8	14.2	1.9	11.9	51.6
1984	5.1	0.1	1.6	47.1	3.9	8.6	33.6
1985	6.3	0.3	1.3	43.6	2.0	3.3	43.2
1986	5.9	0.7	1.3	29.9	1.0	10.5	50.8
1987	5.3	0.8	4.6	36.1	0.5	10.4	42.2
1988	5.3	0.3	2.8	19.6	0.7	8.7	62.5
1989	4.5	1.0	0.5	18.7	0.9	15.9	58.6
1990	8.1	1.0	0.2	16.1	1.4	21.1	51.9
1991	17.4	0.3	1.0	9.7	1.3	14.6	55.6
Mean	7.2	0.6	1.7	27.6	1.5	11.6	49.8

Mann Whitney U-test) in relative percent distribution among the tributaries during the two periods from 18% to 7%.

The percent composition of the major age classes of adult sockeye salmon returning to Bear and Glacier Flats Creeks varied moderately as coefficients of variation ranged between 0.33-0.63 during 1980-1991 (Table 24). Of the four age classes of sockeye salmon observed in these creeks, age-1.2 dominated and ranged in composition between 7-76% (Bear Creek) and 8-80% (Glacier Flats Creek), and averaged 44% and 57%, respectively. Age-1.3 sockeye salmon were second in dominance and ranged between 6-80% at Bear Creek (mean = 34%), and 11-77% at Glacier Flats Creek (mean = 32%). The composition of age-2.2 and age-2.3 averaged less than 20% for both creeks during 1980-1991. In addition, the sizes of the major age classes of adult sockeye salmon returning to Bear Creek and Glacier Flats Creek varied very little (coefficients of variation were equal to or less than 0.10) during 1980-1991 (Table 25). At Bear Creek, age-1.3 sockeye salmon averaged 2.5 kg in weight, and both age-1.2 and age-2.2 averaged 1.7 kg. The mean length of age-1.3 Bear Creek sockeye salmon was 54 cm, and was 48 cm for both age-1.2 and age-2.2 fish. The average weight of these three age classes for Glacier Flats Creek sockeye salmon was nearly identical to Bear Creek. The mean lengths were also similar as age-1.3 Glacier Flats Creek sockeye salmon averaged 53 cm, and both age-1.2 and age-2.2 averaged 48 cm.

Finally, one of the concerns regarding the enhancement project and the distribution of spawners, was the development of only two sockeye salmon stocks (Glacier Flats and Bear Creeks), and the lack of distributing increased production among the other salmon-producing tributaries. As mentioned earlier, from 1976 through 1985 sockeye salmon fingerlings were released directly in Glacier Flats and Bear Creeks using the helicopter ground-release method, and beginning in 1986 the fry were air-dropped in the lake. The recovery of returning hatchery-marked adult sockeye salmon indicate there was

Table 24. Age compositions of adult sockeye salmon sampled from Bear and Glacier Flats Creeks, 1980-1991.

Return year	Percent composition by age class 1.2	1.3	2.2	2.3	Sample size
			Bear Creek		
1980	39	52	8	1	174
1981	25	64	6	5	256
1982	18	80	Trace	2	275
1983	76	14	8	2	174
1984	59	36	5	0	152
1985	75	19	6	Trace	160
1986	65	23	11	Trace	180
1987	40	40	16	4	174
1988	38	33	16	12	340
1989	7	36	43	14	280
1990	42	6	45	7	149
1991	40	8	45	7	500
Mean	44	34	19	5	
Coefficient of variation	0.48	0.63			
			Glacier Flats Creek		
1980	57	41	2	Trace	238
1981	65	35	Trace	Trace	294
1982	23	77	Trace	Trace	251
1983	89	11	Trace	Trace	158
1984	73	24	3	0	62
1985	74	21	4	0	227
1986	55	33	8	4	133
1987	37	45	13	5	94
1988	30	45	17	8	281
1989\a					
1990\b	66	0	24	0	106
1991	59	16	23	2	438
Mean	57	32	12	3	
Coefficient of variation	0.33	0.63			

\a No data collected in 1989.
\b Sampled late in run.

Table 25. Mean weights and lengths of the major age classes of adult sockeye salmon sampled at Bear and Glacier Flats Creeks, 1980-1991.

		Bear Creek					Glacier Flats Creek				
Age class	Return year	Sample size	Average weight (kg)	S.D.	Average length (cm)	S.D.	Sample size	Average weight (kg)	S.D.	Average length (cm)	S.D.
1.3	1980	90	2.5	0.4	54.5	2.0	119	2.3	0.3	53.8	2.4
	1981	217	2.8	0.4	54.9	2.0	122	2.5	0.5	53.8	2.3
	1982	230	2.8	0.4	54.3	2.1	178	2.8	0.5	54.6	2.3
	1983	24	2.6	0.3	56.3	2.3	18	2.4	0.4	54.0	1.8
	1984	55	2.4	0.4	53.9	2.5	15	2.3	0.3	53.3	3.6
	1985	30	2.0	0.3	51.8	3.1	48	2.1	0.4	52.0	3.4
	1986	41	2.4	0.3	53.8	1.8	44	2.7	0.4	55.6	2.3
	1987	70	2.6	0.3	56.1	1.7	42	2.6	0.4	55.3	4.2
	1988	111	2.4	0.4	54.1	2.4	127	2.6	0.3	55.1	2.2
	1989 \a	101	2.4	0.3	54.6	1.8					
	1990 \b	9	2.6	0.3	55.3	1.8					
	1991	41	2.0	0.3	51.7	1.9	72	2.3	0.3	53.0	1.9
Mean			2.5		54.3			2.5		54.1	
C.V.\c			0.10		0.03			0.08		0.02	
1.2	1980	69	1.8	0.2	48.8	1.9	108	1.8	0.2	48.8	1.6
	1981	14	1.8	0.3	48.4	1.8	164	1.7	0.5	48.4	1.9
	1982	43	1.8	0.3	46.7	2.8	70	1.8	0.5	46.4	2.9
	1983	133	1.9	0.4	50.2	2.9	140	1.9	0.3	48.2	2.3
	1984	89	1.8	0.3	48.1	2.8	45	1.6	0.2	46.8	1.7
	1985	75	1.6	0.2	47.9	1.7	74	1.6	0.2	47.4	3.4
	1986	117	1.7	0.3	48.2	2.6	73	1.7	0.3	48.3	2.1
	1987	71	1.4	0.2	46.1	2.2	35	1.5	0.2	46.3	3.5
	1988	133	1.6	0.3	47.7	1.9	83	1.6	0.3	47.6	2.0
	1989 \a	19	1.6	0.3	47.8	2.7					
	1990 \b	63	1.6	0.4	47.7	3.9	70	1.3	0.4	44.2	2.8
	1991	199	1.3	0.2	45.6	2.3	257	1.6	0.3	47.1	2.3
Mean			1.7		47.8			1.6		47.2	
C.V.			0.1		0.0			0.1		0.0	

-continued-

Table 25 continued. Mean weights and lengths of the major age classes of adult sockeye salmon sampled at Bear and Glacier Flats Creeks, 1980-1991.

		Bear Creek					Glacier Flats Creek				
Age class	Return year	Sample size	Average weight (kg)	S.D.	Average length (cm)	S.D.	Sample size	Average weight (kg)	S.D.	Average length (cm)	S.D.
2.2	1980	14	1.9	0.3	49.4	1.7	5	1.9	0.3	49.4	2.4
	1981	20	1.8	0.3	49.0	1.8	3	1.8	0.8	48.5	5.4
	1982										
	1983	13	2.0	0.5	50.5	3.4					
	1984	8	1.7	0.2	48.8	1.6	2	1.7	0.2	45.8	1.1
	1985	6	1.7	0.2	48.9	1.6	4	1.7	0.2	47.6	2.4
	1986	20	1.6	0.2	47.8	2.0	11	1.8	0.3	48.8	3.1
	1987	27	1.4	0.2	46.4	2.7	12	1.5	0.2	46.7	2.4
	1988	56	1.7	0.3	48.4	2.1	49	1.6	0.3	47.9	2.4
	1989 \a	120	1.7	0.3	48.3	1.9					
	1990 \b	67	1.6	0.4	47.0	3.4	25	1.4	0.4	45.0	3.1
	1991	225	1.4	0.2	46.3	2.7	100	1.6	0.3	47.5	2.3
Mean			1.7		48.3			1.7		47.5	
C.V.			0.1		0.0			0.1		0.0	

\a No data collected at Glacier Flats Creek in 1989.

\b Sampled late in run at Glacier Flats Creek, does not include ages 1.1 and 2.1 jacks.

\c Coefficient of variation.

straying of hatchery fish between the two enhanced tributaries each year (Table 26). For example, at Glacier Flats Creek for adult return years 1984-1991, a mean adult recovery rate of 0.15% was observed for fingerlings stocked in Bear Creek. At Bear Creek, a mean adult recovery rate of 0.09% was found for fingerlings originally stocked in Glacier Flats Creek. Although quantitative sampling was not conducted on other tributaries, hatchery marked adults were indeed observed in the other tributaries. Thus, it is evident that straying of returning hatchery adults did occur from both release techniques; however, because air-drops dispersed hatchery fingerlings directly into the lake, a higher percentage of returning hatchery adults may be spawning in the lake.

Hatchery Contribution to the Escapement and the Total Return-- The contribution of hatchery-produced sockeye salmon to the total return incorporated the mortality associated with clipping ventral fins. This was determined from the release of equal numbers of ventral- and adipose-clipped fingerlings in 1984 and 1985, and the return of respective adults in 1987 and 1988. This comparison revealed that a 42% average survival advantage occurred for the control group (adipose-clip fish) over the ventrally-clipped fish (Table 27). This corresponds to an average differential mark mortality factor (DMF) of 1.4, which was slightly less, but close to the average of 1.5 DMF found for smolts (Tables 14 and 15).

The estimated contribution of adult hatchery sockeye salmon to the escapement and total return incorporated a DMF of 1.5, and has been estimated since 1984 (Table 28). The percentage of hatchery fish contributing to the escapement at Glacier Flats and Bear creeks ranged between 12-94% and 17-53%, respectively. Annual estimates of the number of hatchery-produced sockeye salmon in the commercial harvest ranged between 51,000-596,000. In the personal-use and sport fisheries, hatchery sockeye contributed 2,800-18,800 of the annual total catch. The estimated annual number of sockeye salmon adults

Table 26. Recovery rates for RV and LV fin clips at the Glacier Flats and Bear Creek weirs showing the straying of returning hatchery adults between these two creeks, 1984-1991.

Return year	No. fish observed	No. RV recovered\a		Recovery rate (%)	No. LV recovered\b		Recovery rate (%)
				Glacier Flats Creek weir			
1984	12,954	36		0.28%	0		0.00%
1985	24,000	302		1.26%	21		0.09%
1986	17,073	180		1.05%	20		0.12%
1987	8,834	42		0.48%	7		0.08%
1988	14,337	54		0.38%	33		0.23%
1989	8,753	23		0.26%	18		0.21%
1990	3,690	17		0.46%	8		0.22%
1991	4,563	1		0.02%	12		0.26%
Total	94,204	655	Mean	0.52%	119	Mean	0.15%
				Bear Creek weir			
1984	16,695	5		0.03%	72		0.43%
1985	15,681	14		0.09%	153		0.98%
1986	17,119	24		0.14%	138		0.81%
1987	11,096	14		0.13%	39		0.35%
1988	17,045	11		0.06%	25		0.15%
1989	14,310	10		0.07%	24		0.17%
1990	4,600	4		0.09%	15		0.33%
1991	11,608	10		0.09%	44		0.38%
Total	108,154	92	Mean	0.09%	510	Mean	0.45%

\a Glacier Flats Creek sockeye fingerlings marked with a right ventral clip.

\b Bear Creek Creek sockeye fingerlings marked with a left ventral clip.

Table 27. The number of right or left ventral (RV, LV) and adipose (AD) clipped adult sockeye recovered at the Glacier Flats and Bear Creek weirs and the differential mark mortality factors.

Return year	Age class	Number AD clips recovered	Number RV or LV clips recovered\a	Percent ventral clips recovered	Differential mark mortality factor
1987	1.2	37	28 (RV)	43.1	1.32
1988	1.3	44	32 (RV)	42.1	1.38
1988	1.2	33	23 (LV)	41.1	1.43
Mean				42.1	1.38

\a RV clips represent recovered fish from the release of equal numbers of RV and AD Glacier Flats Creek fingerlings in 1984. LV clips represent recovered fish from the release of equal numbers of LV and AD Bear Creek fingerlings in 1985.

Table 28. Estimated number and percentage of hatchery-produced sockeye salmon in the escapement and total return for Tustumena Lake, 1984-1991.

	Return year								Mean
	1984	1985	1986	1987	1988	1989	1990\a	1991\a,f	1984-1991
Kasilof River sonar count (escapement)\b	231,685	505,049	275,963	249,246	203,900 \c	158,206	144,136	238,269	286,636
Bear Creek escapement	54,350	120,400	102,948	71,250	127,532	62,950	46,300	68,880	93,516
Glacier Flats Creek escapement	73,927	121,400	60,615	61,000	40,015	20,150	14,350	12,068	57,646
Other creeks and lake escapement\d	103,408	263,249	112,400	116,996	36,353	75,106	83,486	157,321	135,474
Estimated number and (%) of hatchery-produced fish	8,760	87,032	47,062	36,878	34,786	18,942	8,153	3,485	35,014
returning to Glacier Flats Creek	11.8%	71.7%	77.6%	60.5%	86.9%	94.0%	56.8%	28.9%	69.8%
Estimated number and (%) of hatchery-produced fish	9,378	50,272	50,136	34,060	43,630	33,326	20,001	15,195	36,571
returning to Bear Creek	17.3%	41.8%	48.7%	47.8%	34.2%	52.9%	43.2%	22.1%	44.0%
Estimated number and (%) of hatchery-produced fish	4,191	34,381	5,405	---	---	---	29,157	54,858	18,285
returning to the other creeks	4.1%	13.1%	4.8%	---	---	---	20.2%	23.0%	9.3%
Estimated number and (%) of hatchery-produced fish	22,329	171,685	102,603	70,938	78,416	52,268	57,311	73,538	89,870
in the escapement	9.6%	34.0%	37.2%	28.5%	38.5%	33.0%	39.8%	30.9%	35.9%
Estimated commercial fishing exploitation rate	68.0%	62.2%	84.0%	76.0%	86.5%	70.0%	70.0%	62.1%	82.7%
Estimated commercial harvest\b	524,337	856,471	1,602,827	853,237	981,078	401,000	336,000	405,863	851,545
Estimated number of hatchery-produced fish commercially caught\e	50,534	291,146	595,931	242,840	377,304	132,482	133,599	125,263	278,443
Estimated number of fish caught in personal-use (dipnet and gillnet) and sport fisheries\b	28,908	28,929	50,450	38,697	15,718	14,560	8,094	9,132	27,784
Estimated number of hatchery-produced fish in personal-use and sport fisheries	2,786	9,834	18,757	11,014	6,045	4,810	3,218	2,818	8,469
Estimated number of hatchery-produced fish in the total return	75,649	472,665	717,291	324,792	461,764	189,560	194,129	201,620	376,782

\a Hatchery-produced fish based on respective hatchery smolt contribution (See methods).

\b Estimates from Table 19.

\c The total spawner count (See Table 22) revealed a higher number of sockeye than the sonar count in 1988 (See Table 19), and consequently was used to calculate the contribution of hatchery-produced sockeye to the total return.

\d Represents the difference between Glacier Flats and Bear Creek weir counts and the total spawner count of the seven major salmon-producing tributaries.

\e Hatchery-produced fish in commercial harvest is percent hatchery fish in escapement times commercial harvest.

\f Catch and harvest figures are preliminary.

returning from hatchery fingerling releases during 1984-1991 ranged between 76,000-717,000, averaged 376,782, and totalled nearly 3 million.

Genetic Sampling-- Analysis of the 1987 and 1989 genetic samples collected from adult sockeye salmon spawning in the major tributaries of Tustumena Lake is partially complete. The electrophoresis of sample tissues is complete; however, statistical comparisons have not been finalized. Preliminary analysis of these samples suggests similar results to those found by Grant et al. (1980); sockeye salmon spawning stocks of Tustumena Lake are homogeneous (Carl Burger[3] pers. comm.). However, since the analysis of these samples, advancement of electrophoretic procedures have been made; mainly an increase in the number of detected protein variants. Thus, further testing is recommended and is being planned by the USF&WS.

Limnological Investigations

Heat Budget-- Seasonal mean lake temperatures (1 m) varied annually from 8.3-10.5° C at Station A, 7.2-10.1° C at Station B, and 6.3-8.4° C at Station C (Tables 29-31). The lowest mean lake (all stations combined) temperatures were in 1983 and 1985 (7.3° C), and the highest was in 1991 (9.7° C) when seasonal mean turbidity at each of the three stations was the lowest. The date at which the water temperature reached 4° C at 1 m (initiation of seasonal heating) varied annually from May 1 to June 1 at Station A, from May 4 to June 17 at Station B, and from May 24 to June 19 at Station C. The date of maximum heating (1 m) varied from July 9 to August 26 at Station A, July 9 to August 18 at Station B, and July 7 to August 27 at Station C. Thus, the range in seasonal mean temperature, the initiation of heating, and the date of maximum heating varied dependent upon weather conditions of sunlight and precipitation. These factors can influence lake productivity, and in turn, can effect juvenile

[3]USF&WS, 1011 E. Tutor, Anchorage, AK 99503.

Table 29. Summary of limnological characteristics at Station A in Tustumena Lake for rearing years 1980-1991.

Parameter	Rearing year											
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Turbidity (NTU) 1 m	---	---	---	---	44	45	44	45	39	32	36	31
Seasonal mean water temp. (C @ 1 m)	9.8	9.6	9.2	7.8	8.3	8.3	9.5	8.6	8.4	9.5	9.4	10.5
Date of 1 m water at 4 C	5/28	5/01	5/31	5/10	5/17	5/27	5/20	5/10	6/01	5/28	5/08	5/26
Date of heat maximum (C @ 1 m)	7/25	8/06	8/26	8/04	7/19	7/17	7/29	7/31	8/03	8/01	7/20	7/09
Euphotic zone depth (m)	0.96	1.18	1.20	1.21	1.24	1.25	1.21	1.14	1.28	1.57	1.37	1.50
Total phosphorus (P) 1 m (ug/L)	38.8	50.1	47.5	56.8	45.0	43.7	48.0	52.8	52.8	47.5	44.7	36.7
CTP \a 1 m (ug/L)	2.9	3.4	3.7	4.2	3.5	3.5	3.7	3.9	3.9	3.3	3.5	3.1
Total Kjeldahl N 1 m (ug/L)	130	143	129	157	156	217	141	146	161	168	147	146
Ammonia 1 m (ug/L)	5.7	4.0	6.4	16.4	4.1	4.0	3.8	1.3	1.4	1.9	1.8	6.6
Nitrate + Nitrite 1 m (ug/L)	87.8	95.4	87.1	84.5	88.3	133.3	77.3	84.4	93.4	99.6	91.9	90.5
Atomic ratio of TN to CTP	89:1	83:1	78:1	82:1	98:1	135:1	84:1	83:1	92:1	113:1	89:1	104:1
Silicon 1 m (ug/L as Si)	2,250	2,278	2,186	2,148	2,150	2,495	2,466	2,534	2,470	2,753	2,162	2,106
Alkalinity 1 m (mg/L as CaCO3)	14	14	15	16	16	19	14	14	13	13	14	14
pH units (1 m)	7.0	6.4	7.0	7.2	7.0	7.1	6.9	7.1	6.9	7.2	7.1	7.1
Chlorophyll a (1 m, mean)	1.47	0.29	0.47	0.96	0.86	0.31	0.29	0.28	0.54	0.31	0.27	0.42
Chlorophyll a (1 m, peak)	3.15	0.63	1.17	2.88	1.14	0.66	0.46	0.94	1.21	0.61	0.56	0.85
Diaptomus density (No/m2, mean)	7,039	10,850	1,412	11,411	11,730	1,656	6,835	5,606	8,551	4,196	3,253	13,930
Cyclops density (No/m2, mean)	24,926	23,586	41,415	25,161	24,942	47,836	31,615	44,516	20,028	24,295	28,814	43,556
Diaptomus biomass (mg/m2, mean)	---	34	11	79	31	15	27	39	36	29	21	68
Cyclops biomass (mg/m2, mean)	---	77	99	74	48	93	70	107	55	47	61	114

\a Total phosphorus corrected for turbidity and inorganic particulate phosphorus.

Table 30. Summary of limnological characteristics at Station B in Tustumena Lake for rearing years 1980-1991.

Parameter	Rearing year											
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Turbidity (NTU) 1 m	--	--	--	--	49	44	46	43	40	38	35	33
Seasonal mean water temp. (C @ 1 m)	9.8	8.2	9.2	7.3	8.4	7.2	9.1	7.9	8.2	8.4	9.6	10.1
Date of 1 m water at 4 C	5/31	5/24	6/07	5/04	5/10	6/17	6/11	5/28	6/03	5/23	5/31	5/29
Date of heat maximum (C @ 1 m)	7/25	8/06	7/09	8/04	7/19	7/17	7/29	7/31	7/14	8/18	7/20	7/09
Euphotic zone depth (m)	0.98	1.11	1.12	1.24	1.29	1.15	1.17	1.11	1.24	1.40	1.31	1.50
Total phosphorus (P) 1 m (ug/L)	44.9	52.7	50.3	57.4	45.9	46.0	53.7	56.3	51.9	49.9	46.8	39.4
CTP \a 1 m (ug/L)	3.5	3.9	3.8	4.2	3.6	3.6	4.0	4.1	3.9	3.7	3.6	3.2
Total Kjeldahl N 1 m (ug/L)	137	157	130	151	181	201	140	154	160	159	156	151
Ammonia 1 m (ug/L)	6.9	1.5	5.0	7.5	7.4	1.9	3.0	1.2	1.5	1.6	1.6	5.7
Nitrate + Nitrite 1 m (ug/L)	90.5	98.1	86.2	91.9	89.8	122.6	82.0	95.9	99.5	99.8	97.2	94.2
Atomic ratio of TN to CTP	87:1	88:1	76:1	79:1	112:1	123:1	78:1	83:1	92:1	95:1	90:1	104:1
Silicon 1 m (ug/L as Si)	2,173	2,245	2,132	2,108	2,106	2,477	2,438	2,468	2,451	2,251	2,305	2,095
Alkalinity 1 m (mg/L as CaCO3)	14	14	15	15	17	17	13	14	14	15	14	14
pH units (1 m)	7.0	6.5	7.2	7.2	7.0	6.4	6.9	6.9	7.0	7.2	7.2	7.1
Chlorophyll a (1 m, mean)	0.89	0.20	0.87	0.40	0.56	0.43	0.87	0.26	0.28	0.20	0.29	0.25
Chlorophyll a (1 m, peak)	2.00	0.42	2.75	0.90	0.77	2.03	0.48	0.85	0.68	0.53	0.69	0.74
Diaptomus density (No/m2, mean)	13,237	30,078	720	5,871	22,813	1,582	5,683	1,577	5,701	2,855	4,086	10,941
Cyclops density (No/m2, mean)	35,014	21,593	53,736	37,448	37,466	27,700	39,135	30,004	25,016	22,813	23,423	55,394
Diaptomus biomass (mg/m2, mean)	--	90	5	30	52	9	21	11	16	22	16	59
Cyclops biomass (mg/m2, mean)	--	56	115	111	86	47	87	63	61	46	49	111

\a Total phosphorus corrected for turbidity and inorgnaic particulate phosphorus.

Table 31. Summary of limnological characteristics at Station C in Tustumena Lake for rearing years 1980-1991.

Parameter	Rearing year											
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1889	1990	1991
Turbidity (NTU) 1 m	--	--	--	--	42	46	44	44	43	38	38	33
Seasonal mean water temp. (C @ 1 m)	8.2	--	7.8	7.0	--	6.5	7.2	6.9	6.3	7.2	8.0	8.4
Date of 1 m water at 4 C	5/24	--	6/16	6/19	--	6/15	6/14	6/02	6/14	6/04	6/01	6/04
Date of heat maximum (C @ 1 m)	7/25	--	8/27	7/07	--	7/17	8/21	7/31	7/14	8/01	7/20	7/09
Euphotic zone depth (m)	0.90	1.05	1.09	1.12	1.18	1.21	1.11	1.10	1.15	1.32	1.23	1.40
Total phosphorus (P) 1 m (ug/L)	43.3	51.3	51.7	59.1	43.9	51.2	49.2	54.5	56.2	49.8	51.4	40.3
CTP \a 1 m (ug/L)	3.1	3.9	3.9	4.3	3.5	3.9	3.8	4.0	4.1	3.8	3.8	3.3
Total Kjeldahl N 1 m (ug/L)	125	132	136	142	155	201	148	155	170	164	159	153
Ammonia 1 m (ug/L)	8.3	2.0	4.2	8.9	3.2	1.4	3.0	1.3	1.1	2.4	1.6	5.7
Nitrate + Nitrite 1 m (ug/L)	96.4	100.2	89.4	85.1	97.2	124.3	89.8	98.3	105.2	101.5	100.6	99.2
Atomic ratio of TN to CTP	80:1	75:1	78:1	74:1	100:1	115:1	86:1	85:1	92:1	95:1	83:1	104:1
Silicon 1 m (ug/L as Si)	2,472	2,218	2,106	2,092	2,145	2,441	2,410	2,468	2,377	2,295	2,265	2,079
Alkalinity 1 m (mg/L as CaCO3)	15	13	15	16	16	16	14	13	15	13	14	14
pH units (1 m)	6.4	6.5	7.2	7.2	7.1	6.8	7.0	6.9	6.9	7.3	7.2	7.1
Chlorophyll a (1 m, mean)	1.13	0.09	1.21	0.44	0.47	0.33	0.24	0.21	0.15	0.12	0.20	0.28
Chlorophyll a (1 m, peak)	4.58	0.26	3.70	0.71	1.14	1.20	1.07	1.04	0.65	0.25	0.54	0.59
Diaptomus density (No/m2, mean)	4,957	6,828	1,041	7,269	307	2,087	2,135	1,668	2,620	10,167	13,303	4,840
Cyclops density (No/m2, mean)	34,096	23,624	43,172	59,814	26,868	28,500	56,231	32,015	19,485	26,830	29,504	42,731
Diaptomus biomass (mg/m2, mean)	--	23	5	47	4	6	6	10	7	76	26	34
Cyclops biomass (mg/m2, mean)	--	61	102	172	59	59	135	71	51	50	63	88

\a Total phosphorus corrected for turbidity and inorganic particulate phosphorus.

sockeye production (see section on environmental variables).

Nutrients-- Nitrogen, and in particular phosphorus, are major cellular components of all organisms and can regulate or limit the productivity of organisms in freshwater ecosystems. Concentrations of nitrogen and phosphorus are dynamic because they are constantly being utilized, stored, transformed, and excreted by various aquatic organisms. Other elements such as iron, silica, calcium, and magnesium are essential cellular constituents but are required in relatively low concentrations in relation to their availability in fresh waters. Seasonal mean nutrient concentrations by year are presented in Tables 29-31 for Stations A-C, respectively.

Nitrogen (N) is necessary for aquatic and terrestrial life, and because nitrogen is more abundant it has been generally considered not as limiting to primary production as phosphorus. However, there is growing evidence to suggest that the nitrogen supply when combined with phosphorus levels can significantly change biological responses (regulating photosynthesis and algal standing crop) in lakes (Smith 1982; Elser et al. 1990). There are various inorganic and organic fractions of nitrogen that are measured in water; however, both inorganic forms (ammonia and nitrate + nitrite) are readily utilized by aquatic plants for production. Except under alkaline conditions (pH>9.0), most of the ammonia in freshwater exists in the ionic form known as ammonium (NH_4^+).

Throughout 1980-1991, epilimnetic (1 m) ammonium concentrations in Tustumena Lake ranged from 1.2 to 16.4 µg/L, and the seasonal average of 4 µg/L is low compared to other oligotrophic lakes in Alaska supporting sockeye salmon. Epilimnetic nitrate + nitrite concentrations ranged from 82-133 µg/L, and averaged 95 µg/L. In comparison to other sockeye lakes, nitrate + nitrite concentrations were low to moderate. Total Kjeldahl nitrogen (TKN) which measures organic N and ammonia (ammonium), averaged 155 µg/L and ranged from 125 to 217 µg/L. In comparison, TKN in other sockeye nursery lakes in

Alaska averages ~100 μg/L, indicating that the level of organic N in Tustumena Lake is moderate. Finally, the 1980-1991 average concentration for each of the nitrogen subcomponents varied little among the three stations.

Phosphorus (P) has been considered as a limiting factor of primary productivity in lakes. In addition, biogenic input of nutrients from decomposing salmon carcasses (mainly phosphorus) has been strongly correlated to lake productivity (Gilbert and Rich 1927; Juday et al. 1932; Donaldson 1967). In the analysis of TP samples from glacial lakes, the absorbance (analytical) measurements of turbid solutions are artificially high because of light backscattering, and therefore TP concentrations of turbid lakes need to be adjusted for turbidity, and inorganic particulate phosphorus (Koenings et al. 1987). In Tustumena Lake, total phosphorus corrected for turbidity and inorganic particulate phosphorus (CTP), averaged 3.7 μg/L in the epilimnion and ranged from 2.9 to 4.2 μg/L during 1980-1991. In comparison, total phosphorus in other (clearwater) sockeye nursery lakes in Alaska generally range between 5-10 μg/L.

Finally, for optimum algal growth the atomic ratio of total nitrogen (TKN + nitrate-nitrite) to total phosphorus (TN:TP) is generally between 10-17:1 (Smith 1982). The seasonal TN:CTP ratio in Tustumena Lake averaged 92:1 for the three stations. Smith (1983) found that a TN:TP ratio >29 does not favor the dominance of nitrogen-fixing phytoplankton species e.g., blue-greens which are unusable forms for consumption by zooplankton. Thus, the mean nutrient ratio in Tustumena Lake does not favor conditions for an undesired phytoplankton taxa. In addition, reactive silicon (Si), which is assimilated in large quantities by diatoms in the synthesis of their cell walls or frustules, was found in low concentrations in Tustumena Lake (2,079-2,753 μg/L).

Chlorophyll a-- Seasonal mean chlorophyll a (chl a) levels in the epilimnion of Tustumena Lake ranged from 0.09-1.47 μg/L and averaged 0.45 μg/L for all three stations during 1980-1991 (Tables 29-31). Peak chl a concentrations reached as high as 4.58 μg/L, however, the mean values, relative to other oligotrophic sockeye lakes in Alaska are quite low. The 1980-1991 mean chl a for each of the three stations ranged between 0.46-0.54 μg/L.

Zooplankton Composition, Density, Biomass, and Electivity Indices-- The macrozooplankton community in Tustumena Lake consists of two copepods: *Cyclops columbianus* and *Diaptomus pribilofensis*. Seasonal mean densities (number/m^2) and biomass (mg/m^2) of these two copepods for Stations A-C by year are provided in Tables 29-31. In general, the seasonal mean biomass of *Cyclops* was higher than *Diaptomus*, and *Cyclops* biomass varied more by station than by overall biomass throughout 1981-1991 (Figures 10A and B). In comparison, *Diaptomus* seasonal mean biomass varied both by station and in overall biomass more than *Cyclops* throughout 1981-1991. For all three stations, *Cyclops* biomass ranged from 48-119 mg/m^2 and averaged 78 mg/m^2, *Diaptomus* biomass ranged from 7-52 mg/m^2 and averaged 29 mg/m^2, and combined these copepods ranged in total biomass from 75-171 mg/m^2 and averaged 108 mg/m^2 (Figure 10 C).

There was no apparent relationship between the biomass of either *Cyclops* or *Diaptomus*, or total zooplankton (*Diaptomus* and *Cyclops* combined), and the estimated number of fall fry (Figure 11A and B). This suggests that the food base in terms of numbers and size (biomass) was unaffected by the number of rearing fish in the fall, which is a relative indication of the level of rearing fish throughout the season.

Finally, during 1983, 1985, 1987, and 1988 limited sampling (N=20-37/year) of the diet of age-0 and age-1 sockeye fry collected in the fall indicated a positive electivity indice (active selection) for *Cyclops* and *Diaptomus* (Figure 12). *Cyclops* that were actively selected ranged widely in size interval from 0.50-0.54 mm to 1.40-1.44 mm, and the size intervals of *Diaptomus* that were actively

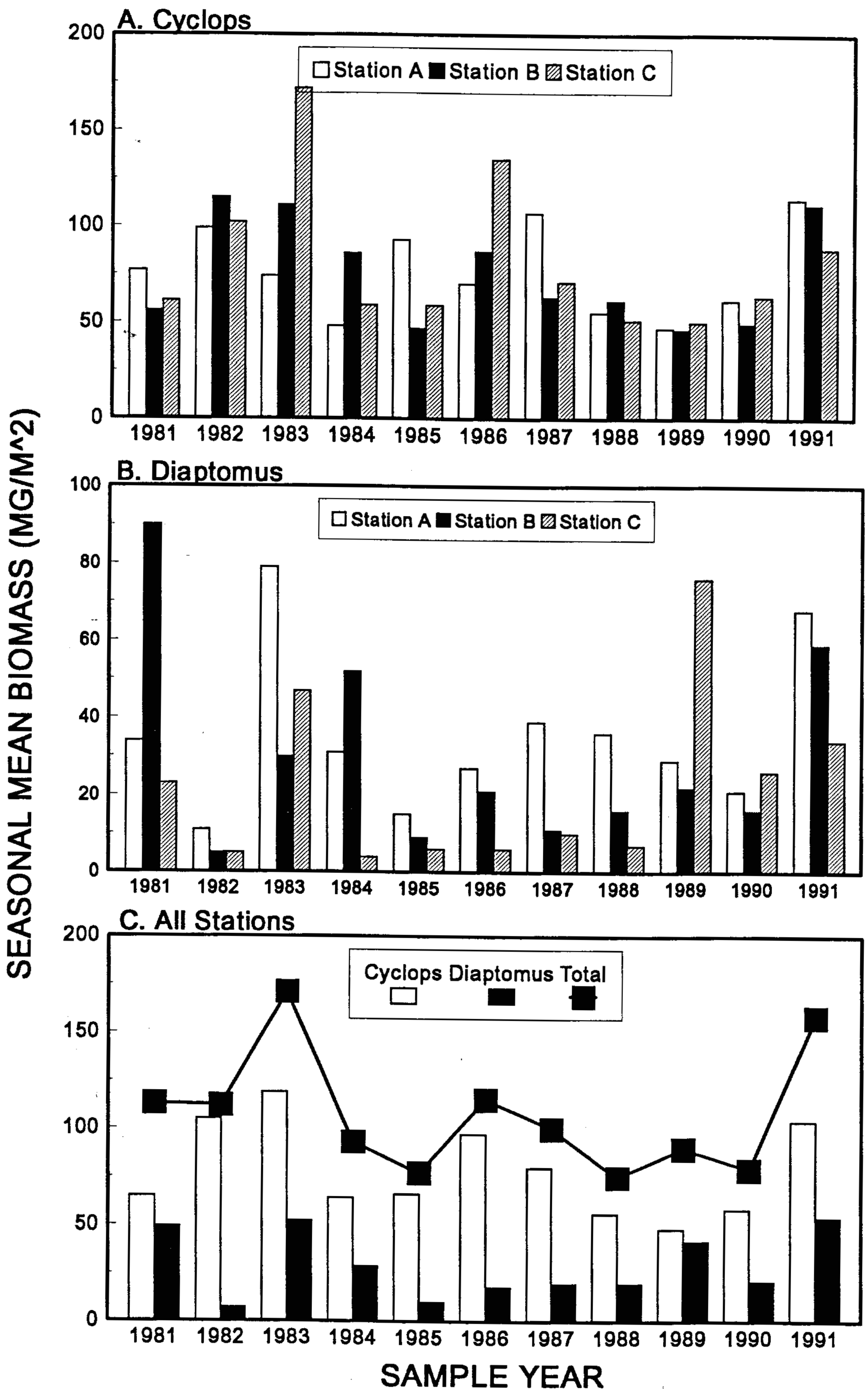
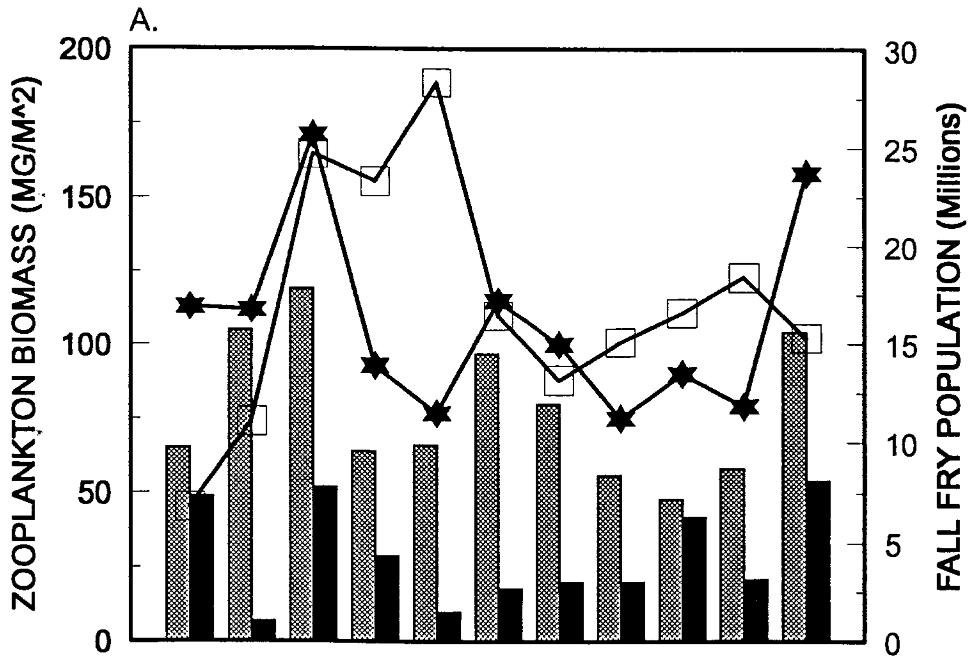


Figure 10. Seasonal mean biomass by year and station for *Cyclops* (A), *Diaptomus* (B), and combined for all three sample stations (C) during 1981-1991.



REARING YEAR	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Cyclops	65.0	105.0	119.0	64.0	66.0	97.0	80.0	56.0	48.0	58.0	104.0
Diaptomus	49.0	7.0	52.0	29.0	10.0	18.0	20.0	20.0	42.0	21.0	54.0
Total	113.0	112.0	171.0	93.0	77.0	115.0	100.0	75.0	90.0	79.0	158.0
Fall fry (millions)	6.8	11.1	24.7	23.3	28.3	16.5	13.2	15.1	16.6	18.4	15.3

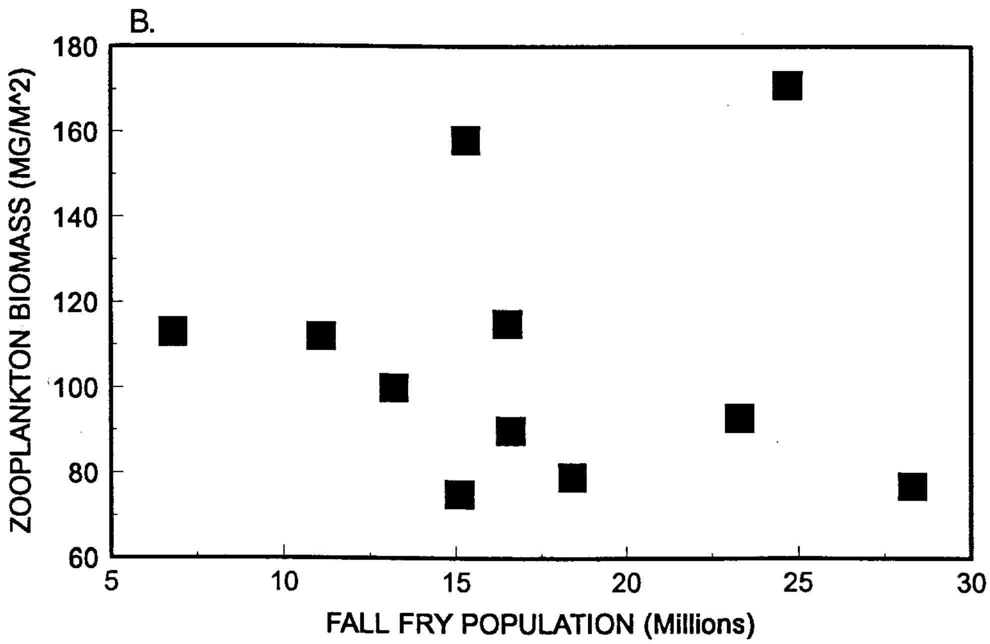


Figure 11. Comparison of zooplankton biomass (*Cyclops*, *Diaptomus*, and total) with the fall fry estimates (A), and the relationship of total zooplankton biomass and fall fry estimates (B) in Tustumena Lake for rearing years 1981-1991.

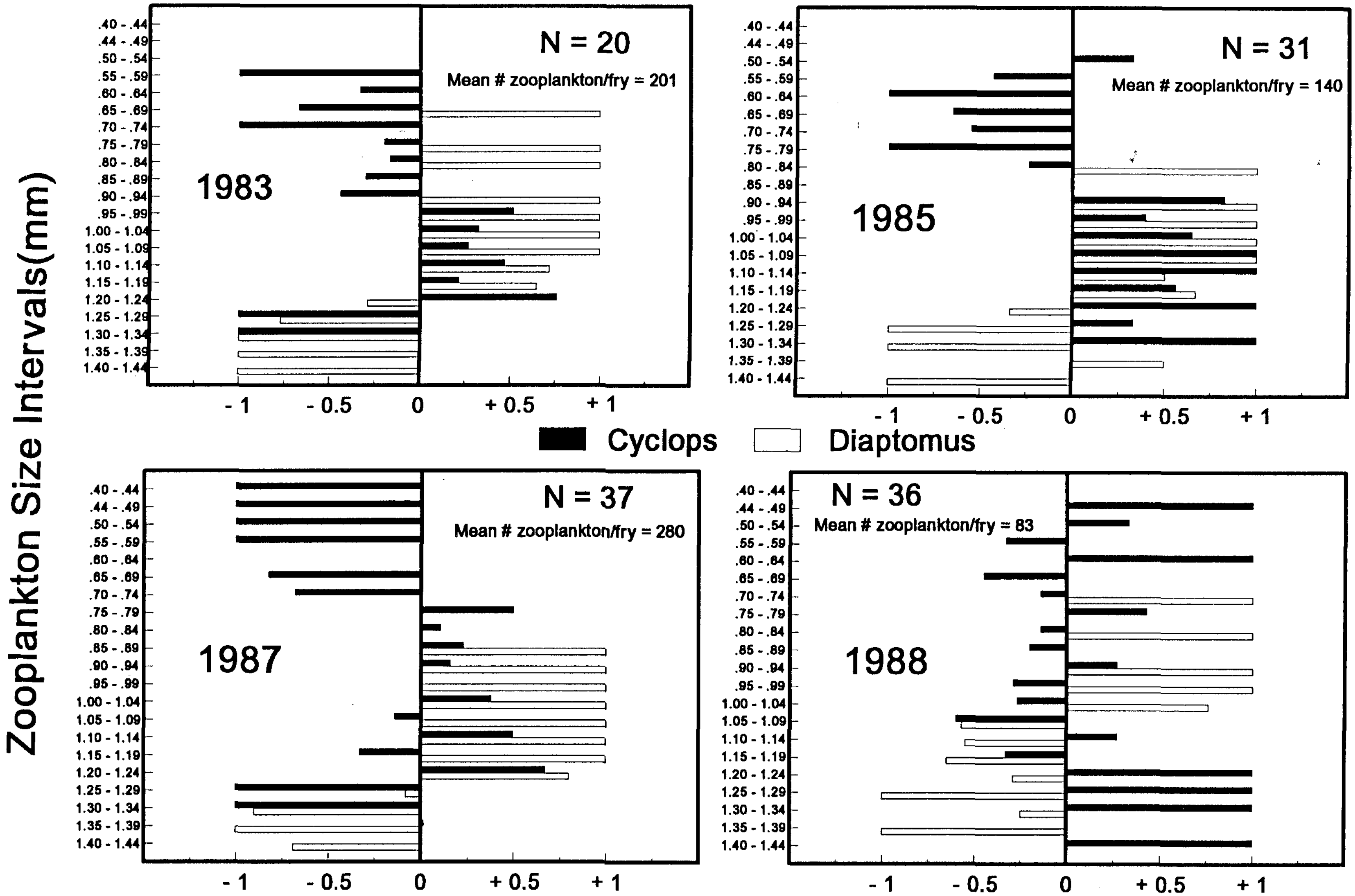


Figure 12. Electivity indices by length increment for *Cyclops* and *Diaptomus* consumed by juvenile sockeye salmon in Tustumena Lake in the fall of 1983, 1985, 1987, and 1988.

preyed upon also had a broad range from 0.65-0.69 mm to 1.35-1.39 mm. Thus, there did not appear to be a preference for *Cyclops* or *Diaptomus*, or active selection for certain size intervals. Moreover, the mean number of zooplankton (*Cyclops* and *Diaptomus* combined) per fry ranged from 83 in 1988 to 280 in 1987. In 1983, 1985, 1987, and 1988, the mean number of *Cyclops* per fry was 43, 98, 82, and 66 respectively, while the mean number of *Diaptomus* per fry was 158, 42, 198, and 17 respectively. Thus, during 1985 and 1987 sockeye fry contained more *Cyclops*, and in 1983 and 1987 the fry contained more *Diaptomus*.

Environmental Variables-- To evaluate the effects of diverse rearing environments on smolt production and to evaluate density-dependent or density-independent rearing in Tustumena Lake; six parent-years (1979 through 1984) when sockeye salmon escapements were relatively consistent were used for analysis (Koenings et al. 1988). Six juvenile sockeye salmon performance variables were tested for significant correlations with nine secondary trophic-level variables, two primary-productivity variables, and nine environmental variables by either univariate or multivariate regression analysis.

Implicit in the evaluation of the type of rearing model operating in Tustumena Lake was the concept of explaining variation in the six fish performance variables by correlation to the other trophic-level variables and environmental parameters. In a density-dependent rearing model, variation in fish performance would be correlated to trophic-level changes; whereas, in a density-independent model, correlations to other trophic-level variables should not exist but correlations to environmental variables should be evident.

Preliminary analysis indicate that the variables directly related to the juvenile food chain such as chlorophyll a, zooplankton density, and zooplankton biomass accounted for only 1 to 6% of the variation in fish performance variables. In contrast, environmental variables such as the onset of spring heating, seasonal precipitation, and euphotic zone depth, accounted for between 84-94% of the variation in wild smolt production. As euphotic zone depth was consistently and predominantly correlated to fish performance variables, it was deleted from the correlation matrix to determine the change in influence of the other parameters on fish performance. Again, environmental variables accounted for most of the variation but now accounted for 44 to 73% of the variation in fish performance, while food-chain variables such as chlorophyll a and zooplankton density and biomass accounted for 18% to 46% of the variation.

As food-chain variables did appear to account for a larger percentage of variation in juvenile fish variables without the inclusion of euphotic zone depth in the correlation matrix, it was questioned whether there was a direct link between these two variables. What Koenings et al. (1988) found was that the variation in density and biomass of zooplankton was highly correlated to environmental variables such as the delay in the initiation of spring heating, the duration of the heating period, lake temperature, and precipitation. In fact, when the environmental variables were removed from the correlation matrix none of the zooplankton variables met the statistical acceptance for explaining any changes in fish performance. Thus, the observed variation in fish performance variables by zooplankton were due to co-variation from changing environmental conditions and therefore no direct cause-and-effect could be established between zooplankton variables and fish density or growth.

As previously mentioned, a highly significant relationship was found between euphotic zone depth and the six fish performance variables. In addition, Koenings et al. (1988) found a similar relationship between euphotic zone depth, which influences in-lake rearing conditions, and smolt survival. In fact, 88% of the annual variation in this survivorship was explained by changes in the euphotic zone depth, which permitted the comparison of predicted smolt production with the observed. Consequently, Koenings et al. (1988) found that the predicted smolt production based on yearly changes in euphotic volume corresponded exceptionally well to the actual smolt production during 1979-1984.

SUMMARY

During 1981-1991, production of juvenile sockeye salmon in Tustumena Lake varied widely as total smolt biomass ranged between 7,200-52,500 kg (Table 13). This smolt biomass production occurred from parental escapements ranging from 160,000-500,000 adults (Table 19), and hatchery releases ranging from 6-17 million fingerlings (Table 4). The total hatchery contribution (both age-1 and age-2 smolts) to the smolt production varied from a high of 38% in 1983 and 1987 to a low of 2.5% in 1990, and averaged 24% (Table 16). Since 1984, the estimated number of hatchery-produced sockeye salmon in the commercial harvest ranged between 51,000-596,000. In the personal-use and sport fisheries, hatchery sockeye contributed 2,800-18,800 of the annual total catch. The estimated number of sockeye salmon adults returning from hatchery fingerling releases during 1984-1991 ranged between 76,000-717,000, averaged 377,000, and totalled nearly 3 million.

Although smolt biomass production varied over a wide range of adult escapements, the production of wild smolt biomass during 1981-1991 was not found to be significantly ($p > .05$) related to escapement levels (Figure 8A). However, a significant ($r^2 = 0.56$; $p = .012$) relationship was found between escapements and the percentage of wild pre-smolts that heldover in the lake for an additional year of rearing (Figure 8B). In comparison, there was no significant ($p > .05$) relationship between the number of hatchery fingerlings released and hatchery smolt biomass (Figure 9A), nor with the percentage of hatchery pre-smolts that heldover in the lake for an additional year of rearing (Figure 9C). In addition, during smolt years 1981-1986, the composition of age-

1 sockeye smolts was relatively consistent; ranging between 70-84% (Table 11), and averaging nearly 80%. In 1987, the composition of age-1 smolts drastically declined to 23%, and increased to >45% for 1988-1991. The change in composition of age-1 smolts may not be an exclusive density-dependent effect, as in the fall of 1986 the population estimate of age-0 fingerlings was substantially less than other years (Table 7). As a result, these findings suggest that the initial hypothesis that sockeye salmon production in Tustumena Lake is exclusively density-dependent is incorrect and strongly suggest that density-independent factors must influence production. However, there could be subsequent density-dependent effects resulting from poor environmental conditions.

In Tustumena Lake instead of finding typical food-chain linkages leading to fish production; energy transfer appears to bypass preceding trophic levels. That is, if sockeye salmon rearing in Tustumena Lake operated in an exclusive density-dependent fashion, the model would resemble the middle model in Figure 13B (Koenings et al. 1988). However, as Koenings et al. (1988) found few significant energy transfers between trophic levels; sockeye salmon production primarily appears to be density-independent. In the density-independent model there are direct and significant correlations between environmental factors such as heat budget parameters and light penetration, and rearing fish (Figure 13C). Consequently, in-lake environmental factors appear to influence freshwater sockeye production in Tustumena Lake, and should be given higher regard in assessing the potential production of sockeye salmon in this lake (as well as other glacier lakes), and the effectiveness/impacts of hatchery stocking projects.

Finally, a major concern relative to the increase enhanced production of sockeye salmon in Tustumena Lake was the potential change in distribution of spawners in the non-enhanced (as well as enhanced) tributaries of Tustumena Lake resulting from increased harvests in the commercial fishery. This was assessed by weir counts and peak spawning survey counts. Although counting

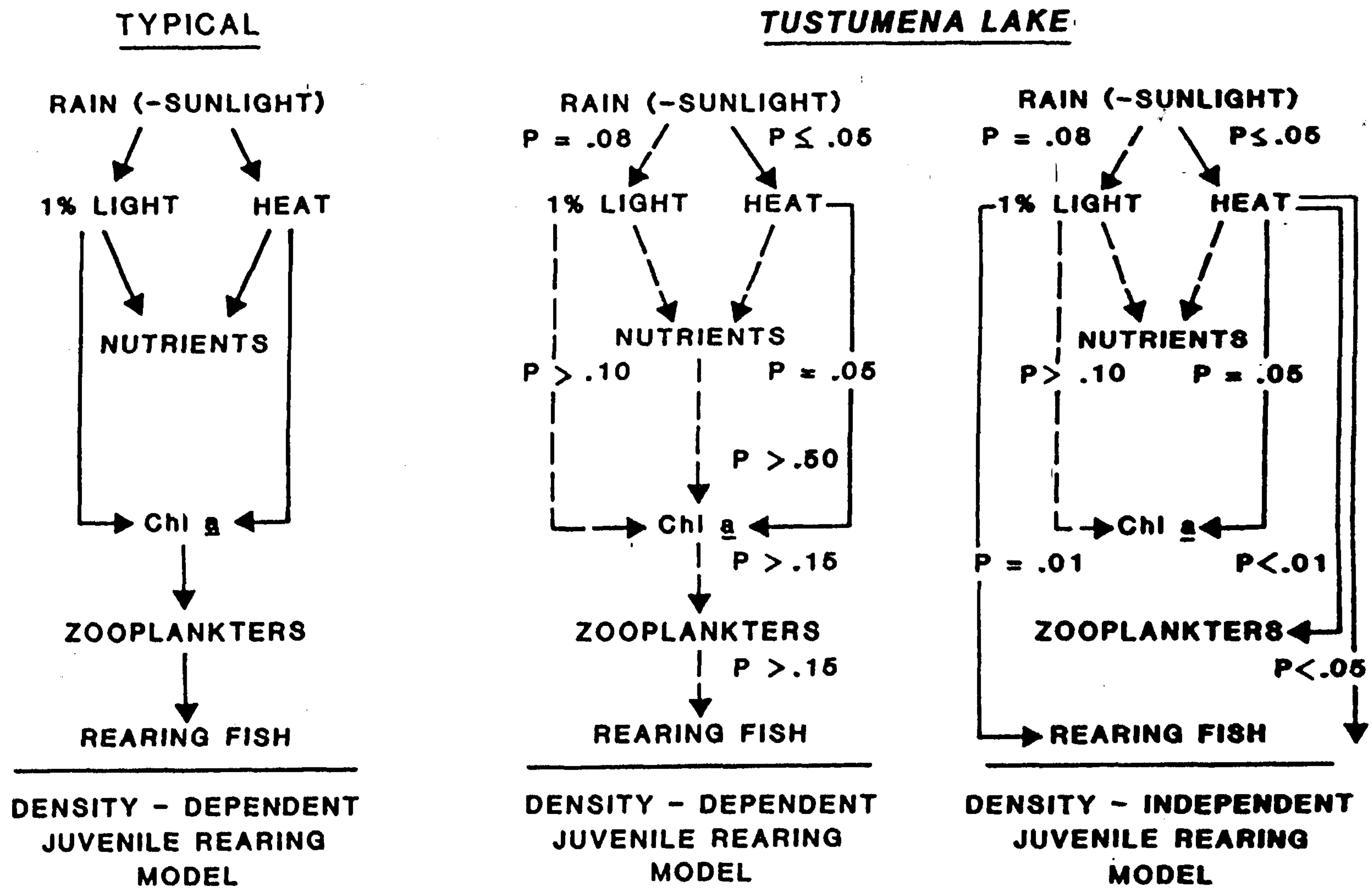


Figure 13. Comparison of energy flow models through successive trophic levels in a typical density-dependent sockeye nursery lake (A), and in Tustumena Lake based on a density-dependent evaluation (B), and on a density-independent evaluation (C). Solid lines indicate significant energy transfers, and dashed lines indicate insignificant transfers (p=.05).

techniques varied among the tributaries, the same technique was used on each tributary each year, establishing an index for comparison. The results of this study indicated that during 1975-1991, two of the seven major sockeye salmon-producing tributaries drastically changed in relative spawner distribution. That is, in Glacier Flats Creek, because poor spawning area limits natural production, it was not surprising for spawner counts to dramatically increase from a mean of 16,600 (1975-1983) to 50,725 after substantial returns of hatchery fish (1984-1991) (Table 22). Correspondingly, the percent distribution of spawners in Glacier Flats Creek changed significantly ($p < .05$) after large hatchery returns from 14% during 1975-1983 to 28% for 1984-1991 (Table 23). Contrary to the enhanced stock at Glacier Flats Creek, the non-enhanced sockeye salmon of Nikolai Creek decreased significantly in percent distribution before and after large hatchery returns from 18% to 7%. However, it is unlikely that this could have resulted from the enhancement project in Tustumena Lake (e.g. increased commercial harvest), as sockeye salmon of Nikolai Creek return earlier than the other stocks (King and Tarbox 1987) and are only partially subjected to the commercial fishery.

ACKNOWLEDGEMENTS

The authors would like to acknowledge former USF&WS biologists Larry Van Ray, Jack Dean, the late Gerald Gray, and current USF&WS staff for logistical support and cooperation in conducting field work. In addition, Loren Flagg, former Area Biologist with ADF&G, is recognized for project planning, project initiation, and past analysis of sockeye salmon information. Ken Tarbox of the ADF&G Commercial Fish Division provided useful comments to the draft of this report. Former project biologist Dave Waite of ADF&G, former ADF&G employee Dave Litchfield, Gary Todd and Pat Shields of ADF&G, and staff of the Crooked Creek Hatchery are thanked for conducting a major portion of the field work. In addition, Gary Todd compiled many of the summary tables. The staff of the Limnology Laboratory, in particular, Jim and John Edmundson are acknowledged for the analysis of water and zooplankton samples. Dr. Richard Thorne of BioSonics Inc. and associates conducted the hydroacoustic surveys through 1987 and analyzed data from all the surveys. Finally, funding for this project was supported through Anadromous Fish Conservation Funds (Department of the Interior - USF&WS), State of Alaska general funds through the Division of Fisheries Rehabilitation, Enhancement, and Development of the ADF&G, and general funds of the USF&WS.

REFERENCES

Bazigos, G. 1976. The design of fisheries statistical surveys - inland waters. FAD Fish. Tech. Paper No. 3, Supl. 1. 44 p.

Brocksen, R. W., G. E. Davis, and C. E. Warren. 1970. Analysis of trophic processes on the basis of density-dependent functions. P. 468-499. In J. A. Steel [ed.]. Marine food chains. Oliver and Boyd, Edinburgh.

Cross, B. A., W. E. Goshert, and D. L. Hicks. 1987. Origins of sockeye salmon in the fisheries of upper Cook Inlet in 1984 based on analysis of scale patterns. Alaska Department of Fish and Game. Division of Commercial Fisheries. Tech. Rep. No. 87-01. Juneau, Alaska. 120 p.

Crowther, J., B. Wright, and W. Wright. 1980. Semi-automated determination of total phosphorus and total Kjeldahl nitrogen in surface waters. Anal. Chem. Acta. 119:313-321.

Davis, R. 1985. Alaska Department of Fish and Game Genetic Policy. Alaska Department of Fish and Game. FRED Div. Special Report. Juneau, Alaska. 25 p.

Donaldson, J. R. 1967. The phosphorus budget of Illiamna Lake, Alaska, as related to the cycle abundance of sockeye salmon. Ph. D. Thesis, Univ. Washington, Seattle, WA. 141 p.

Eggers, D. M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnol. Oceanogr. 23:1114-1125.

Eisenreich, S.J., R. T. Bannerman, and E. D. Armstrong. 1975. A simplified phosphorus analysis technique. Environ. Letters. 9:43-53.

Elser, J. J., E. R. Marzolf, and C. R. Goldman. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Can. J. Aquat. Sci. 47:1468-1477.

Flagg, L. B. 1983. Sockeye salmon smolt studies, Kasilof River Alaska, 1981. Alaska Department of Fish and Game. FRED Div. Rep. Ser. No. 11. Juneau, Alaska. 31 p.

Flagg, L. B., M. J. Owecke, and D. C. Waite, 1984. Sockeye salmon smolt studies, Kasilof River, Alaska, 1982. Alaska Department of Fish and Game. FRED Div. Rep. Ser. No. 27. Juneau, Alaska. 37 p.

Flagg, L. B., K. E. Tarbox, and J. Dean. 1985. Sockeye salmon investigations, Tustumena Lake system, Alaska. Alaska Department of Fish and Game. Prog. Rep. No. 3. Upper Cook Inlet Data Rep. No. 85-1. Soldotna, Alaska. 50 p.

Flagg, L. B., K. E. Tarbox, D. C. Waite, and J. Dean. 1986. Sockeye salmon investigations, Tustumena Lake system, Alaska. Alaska Department of Fish and Game. Prog. Rep. No. 4. Upper Cook Inlet Data Rep. No. 86-3. Soldotna, Alaska. 49 p.

Flagg, L. B., G. A. Gray, J. P. Koenings, and K. E. Tarbox. 1987. Summary of the results for Tustumena Lake sockeye salmon investigations, 1981-86. Alaska Department of Fish and Game. Prog. Rep. No. 5. Unpublished. Soldotna, Alaska. 121 p.

Foerster, R. E. 1944. The relation of lake population density to size of young sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. Bull. 162:422 p.

FRED Staff. 1983. Fish Culture Manual. Alaska Department of Fish and Game. FRED Div. Special Report. Juneau, Alaska. 90 p.

Gilbert, C. H. and W. H. Rich. 1927. Investigations concerning the red salmon runs to the Karluk River, Alaska. Fish. Bull. 43:1-69.

Gjernes, T. 1979. A portable midwater trawling system for use in remote lakes. Dept. Fish. and Oceans Tech. Rep. Ser. 10 p.

Grant, W. S., G. B. Milner, P. Krasnowski, and F. M. Utter. 1980. Use of biochemical genetic variants for identification of sockeye salmon (*Oncorhynchus nerka*) stocks in Cook Inlet, Alaska. Can. J. Fish. Aquat. Sci. 37:1236-1247.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven. 302 p.

Johnson, W. E. 1965. On the mechanism of self-regulation of population abundances in (*Oncorhynchus nerka*). Mitt. Intern. Verein. Limnol. 31:66-87.

Juday, C., W. H. Rich, G. I. Kemmerer, and A. Mann. 1932. Limnological studies of Karluk Lake, Alaska, 1926-1930. Fish. Bull. 47: 407-436.

King, B. E. and K. E. Tarbox. 1984. Upper Cook Inlet (*Oncorhynchus* spp.) escapement studies, 1983. Alaska Department of Fish and Game. Division of Commercial Fish. Tech. Data Rep. No. 122. Juneau, Alaska. 152 p.

King, B. E. and K. E. Tarbox. 1987. Upper Cook Inlet (*Oncorhynchus* spp.) escapement studies, 1987. Alaska Department of Fish and Game. Division of Commercial Fish. Tech. Data Rep. No. 201. Juneau, Alaska. 200 p.

King, B. E. and K. E. Tarbox. 1991. Upper Cook Inlet salmon escapement studies, 1990. Alaska Department of Fish and Game. Division of Commercial Fish. Tech. Data Rep. No. 91-21. Juneau, Alaska. 62 p.

Koenings, J. P. and R. D. Burkett. 1987. Population characteristics of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes,euphotic volume, fry density, and forage base within Alaska lakes, p. 216-234. In H. D. Smith, L. Margolis, and C. C. Wood [eds.]. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96 p.

Koenings, J. P., J. E. Edmundson, G. B. Kyle, and J. M. Edmundson. 1987. Limnological field and laboratory manual: methods for assessing aquatic production. Alaska Department of Fish and Game. FRED Div. Rep. Ser. No. 71. Juneau, Alaska. 212 p.

Koenings, J. P., J. A. Edmundson, and G. B. Kyle. 1988. Density-dependent environmental influences on sockeye salmon (*Oncorhynchus nerka*) fry recruitment and smolt production in Tustumena Lake, Alaska. Can. J. Fish. Aquat. Sci. In review.

Kyle, G. B. 1983. Crescent Lake sockeye salmon smolt enumeration and sampling, 1982. Alaska Department of Fish and Game. FRED Div. Rep. Ser. No. 17. Juneau, Alaska. 24 p.

Kyle, G. B. 1987. Tustumena Lake sockeye salmon studies. Alaska Department of Fish and Game. Federal Aid Annual Rep. AFS-50-3. Juneau, Alaska. 25 p.

Kyle, G. B. 1988a. Tustumena Lake sockeye salmon studies. Alaska Department of Fish and Game. Federal Aid Annual Rep. AFS-50-4. Juneau, Alaska. 28 p.

Kyle, G. B. 1988b. Comparison of fall acoustic population estimates of juvenile sockeye salmon (*Oncorhynchus nerka*) in Alaskan lakes with smolt estimates from trap catches. Presented at the 1988 annual meeting of the North Pacific International Chapter of the American Fisheries Society. Hood Canal, WA.

Kyle, G. B. 1989. Tustumena Lake sockeye salmon studies. Alaska Department of Fish and Game. Federal Aid Annual Rep. AFS-50-5. Juneau, Alaska. 30 p.

Kyle, G. B. 1990. Summary of acoustically-derived population estimates and distributions of juvenile sockeye salmon (*Oncorhynchus nerka*) in 17 lakes of southcentral Alaska, 1982-1987. Alaska Department of Fish and Game. FRED Div. Rep. Ser. No. 104. Juneau, Alaska. 47 p.

Kyle, G. B., J. P. Koenings, and B. M. Barrett. 1988. Density-dependent, trophic level responses to an introduced run of sockeye salmon (*Oncorhynchus nerka*) at Frazer Lake, Kodiak Island, Alaska. Can. J. Fish. Aquat. Sci. 45:856-867.

Levy, D. A. 1987. Review of the ecological significance of diel vertical migrations of juvenile sockeye salmon (*Oncorhynchus nerka*). p.44-52. In H. D. Smith, L. Margolis, and C. C. Wood [eds.]. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96 p.

Murphy, J. and J. P. Riley. 1962. A modified single solution method for the determination of phosphorus in natural waters. Anal. Chem. Acta. 27:31-36.

Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon on the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27:281-316.

Nunnallee, E. P. 1980. Application of an empirically scaled digital echo integrator for assessment of juvenile sockeye salmon populations. Ph. D. thesis. University of Washington. Seattle, Washington. 151 p.

Nunnallee, E. P. and O. A. Mathisen. 1972. An acoustic survey of Lake Wenatchee, Washington. Circular No. 72-13. University of Washington. College of Fisheries. Fisheries Research Institute. 43 p.

Rawson, K. 1984. An estimate of the size of a migrating population of juvenile salmon using an index of trap efficiency obtained by dye marking. Alaska Department of Fish and Game. FRED Div. Rep. Ser. No. 28. Juneau, Alaska. 23 p.

Reed, D. 1981. Mark recovery in a single fishery of single year returns. Alaska Department of Fish and Game. FRED Division. Unpublished. Anchorage, Alaska.

Reimann, B. 1978. Carotinoid interference in the spectrophotometric determination of chlorophyll degradation products from the natural populations of phytoplankton. Limnol. Oceanogr. 23:1059-1066.

Schindler, D. W. 1971. Light, temperature, and oxygen regimes of selected lakes in the experimental lakes area, Northwestern Ontario. J. Fish. Res. Board Can. 28:157-169.

Shields, P. A. and G. B. Kyle. 1990. Tustumena Lake sockeye salmon studies. Alaska Department of Fish and Game. Federal Aid Annual Rep. AFS-50-6. Juneau, Alaska. 24 p.

Smith, V. H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: An empirical and theoretical analysis. Limnol. Oceangr. 27(6):1101-1112.

Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 12. Vol. 221. No. 4611. p. 669-670.

Stainton, M. P., M. J. Capel, and F. A. J. Armstrong. 1977. The chemical analysis of freshwater. Can. Spec. Publ., 2nd ed. Winnipeg, Canada. 25:180 p.

Strickland, J. D. H. and T. R. Parsons. 1972. A practical handbook of seawater analysis, 2nd ed. Fish. Res. Board Can. Bull. 167:310 p.

Tarbox, K. E., B. E. King, and D. L. Waltemyer. 1983. Cook Inlet sockeye salmon studies. Alaska Department of Fish and Game. Division of Commercial Fish. Completion report for period July 1, 1977 to June 30, 1982. Unpublish. Juneau, Alaska.

Tarbox, K. E., L. B. Flagg, L. C. Van Ray, and J. Dean. 1984. Sockeye salmon investigations, Tustumena Lake, Alaska. Alaska Department of Fish and Game. Prog. Rep. No. 2. Upper Cook Inlet Data Rep. No. 84-5. Soldotna, Alaska. 30 p.

Thorne, R. 1983. Hydroacoustics. Chapter 12. In L. Nielsen and D. Johnson (eds.). Fisheries Techniques. American Fisheries Society. Bethesda, Maryland.

Thorne, R. E. 1988. An empirical evaluation of the duration-in-beam technique for hydroacoustic estimation. Can. J. Fish. Aquat. Sci. 45:1244-1248.

Thorne, R. E. and G. L. Thomas. 1981. Hydroacoustic measurements of the density and distribution of juvenile sockeye salmon in Tustumena Lake. Final report to USF&WS. Contract No. 14-16-0007-81-5206. University of Washington. Fisheries Research Institute. Seattle, Washington. 29 p.

Thorne, R. E. and G. L. Thomas. 1982. Hydroacoustic measurements of the density and distribution of juvenile sockeye salmon in Tustumena Lake, Alaska, during 1983. Final report to USF&WS. Contract No. 14-16-0007-81-5271. University of Washington. Fisheries Research Institute. Seattle, Washington. 28 p.

Todd, G. L. and G. B. Kyle. 1991. Tustumena Lake sockeye salmon studies. Alaska Department of Fish and Game. Federal Aid Annual Rep. AFS-50-7. Juneau, Alaska. 28 p.

Utter, F. M., H. O. Hodgins, and F. W. Allendorf. 1974. Biochemical genetic studies of fishes: potentialities and limitations, p. 213-237. In D. Malins [ed.]. Biochemical and biophysical perspectives in marine biology. Vol. 1. Academic Press, San Francisco.

Van Ray, L. C., K. E. Tarbox, L. B. Flagg, and J. P. Koenings. 1983. Production of sockeye salmon in the Tustumena Lake system, Alaska. Prog. Rep. No. 1. U.S. Fish and Wildlife Service. Unpublished. Soldotna, Alaska. 15 p.

Wilson, M. S. 1959. Calanoida. p. 738-794. In W. T. Edmondson [ed.]. Fresh-water biology, 2nd ed. John Wiley and Sons, New York.

Yeatman, H. C. 199. Cyclopoida. p. 795-815. In W. T. Edmondson [ed.]. Fresh-water biology, 2nd ed. John Wiley and Sons, New York.

APPENDIX

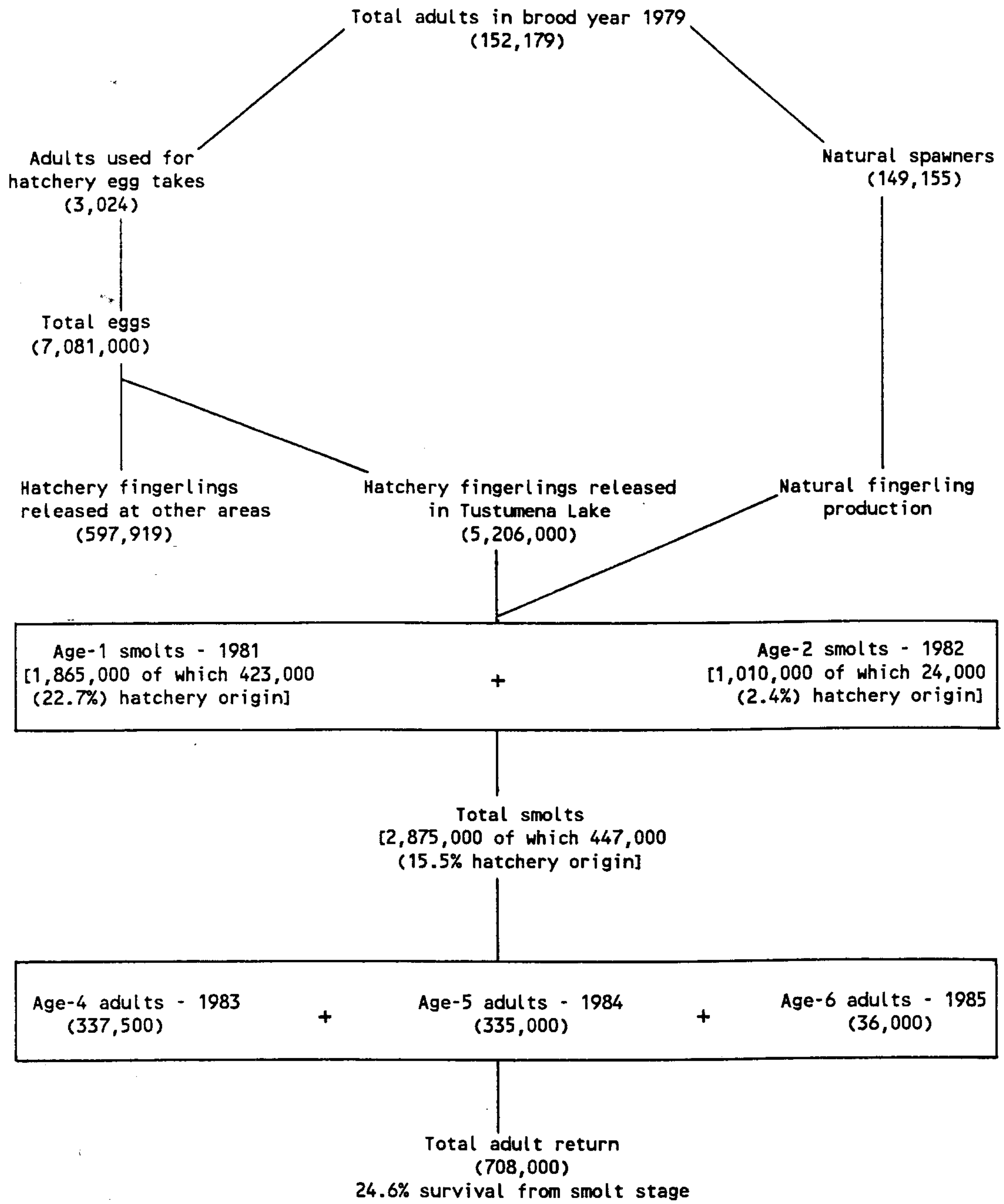


Figure A1. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1979.

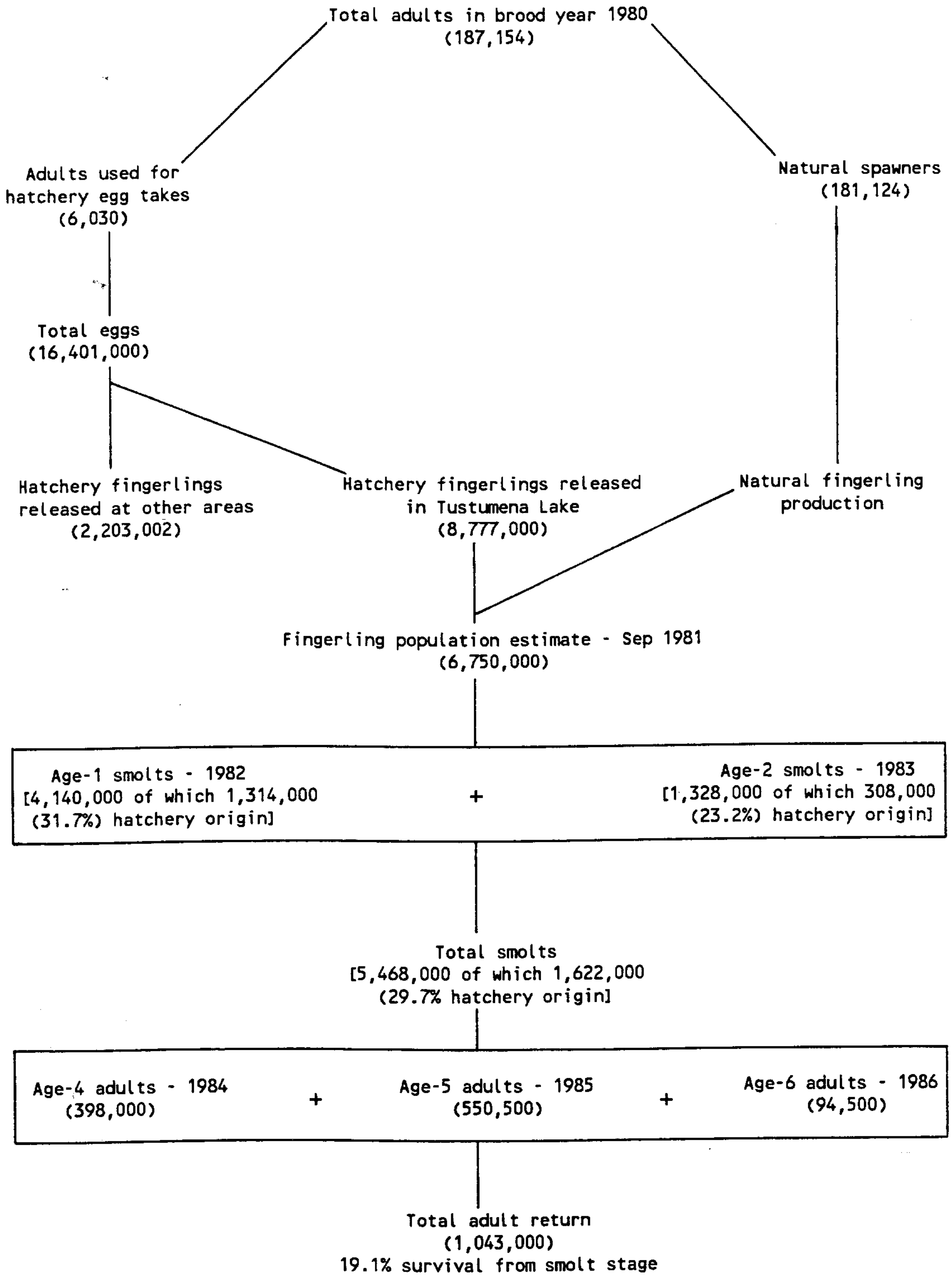


Figure A2. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1980.

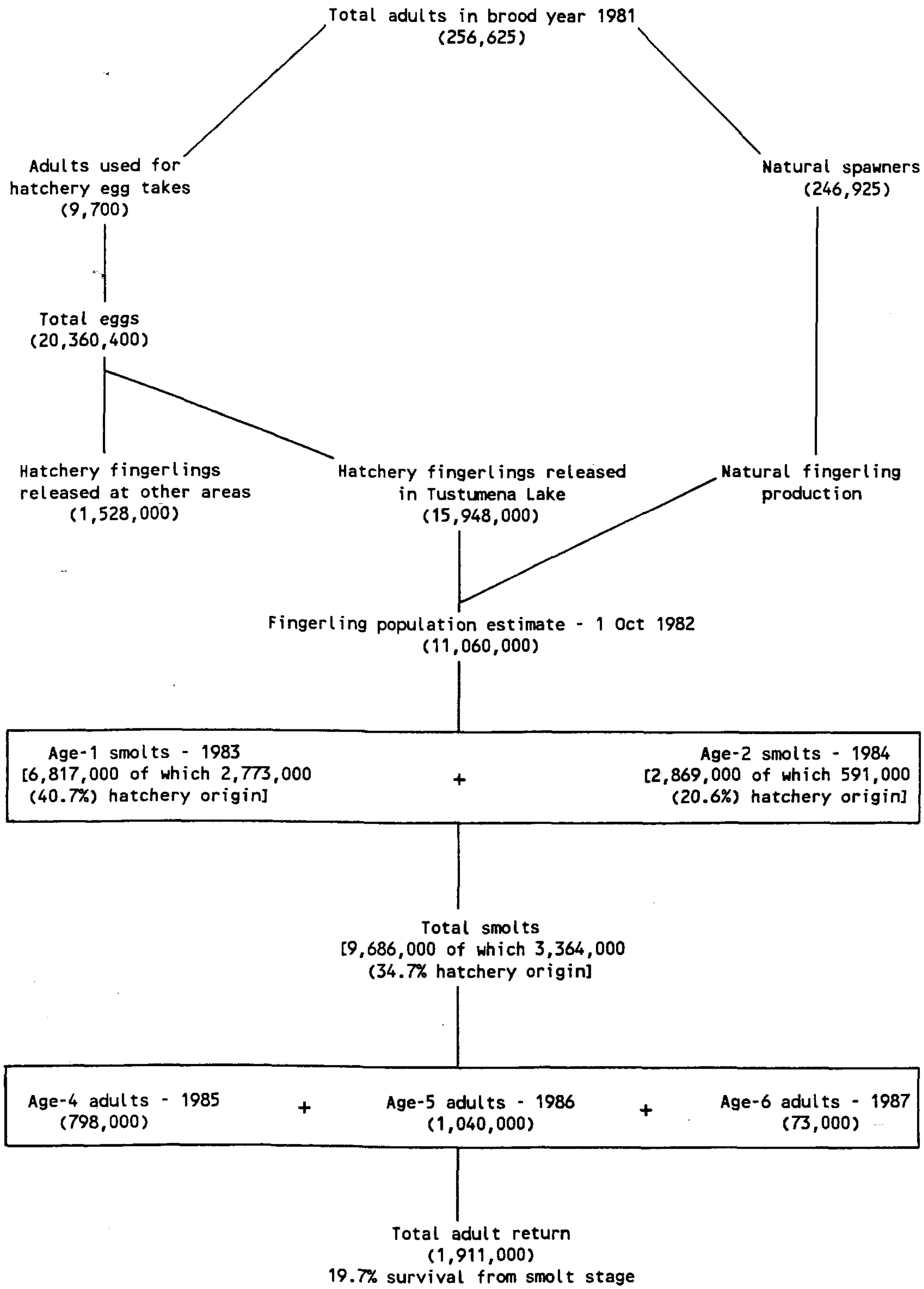


Figure A3. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1981.

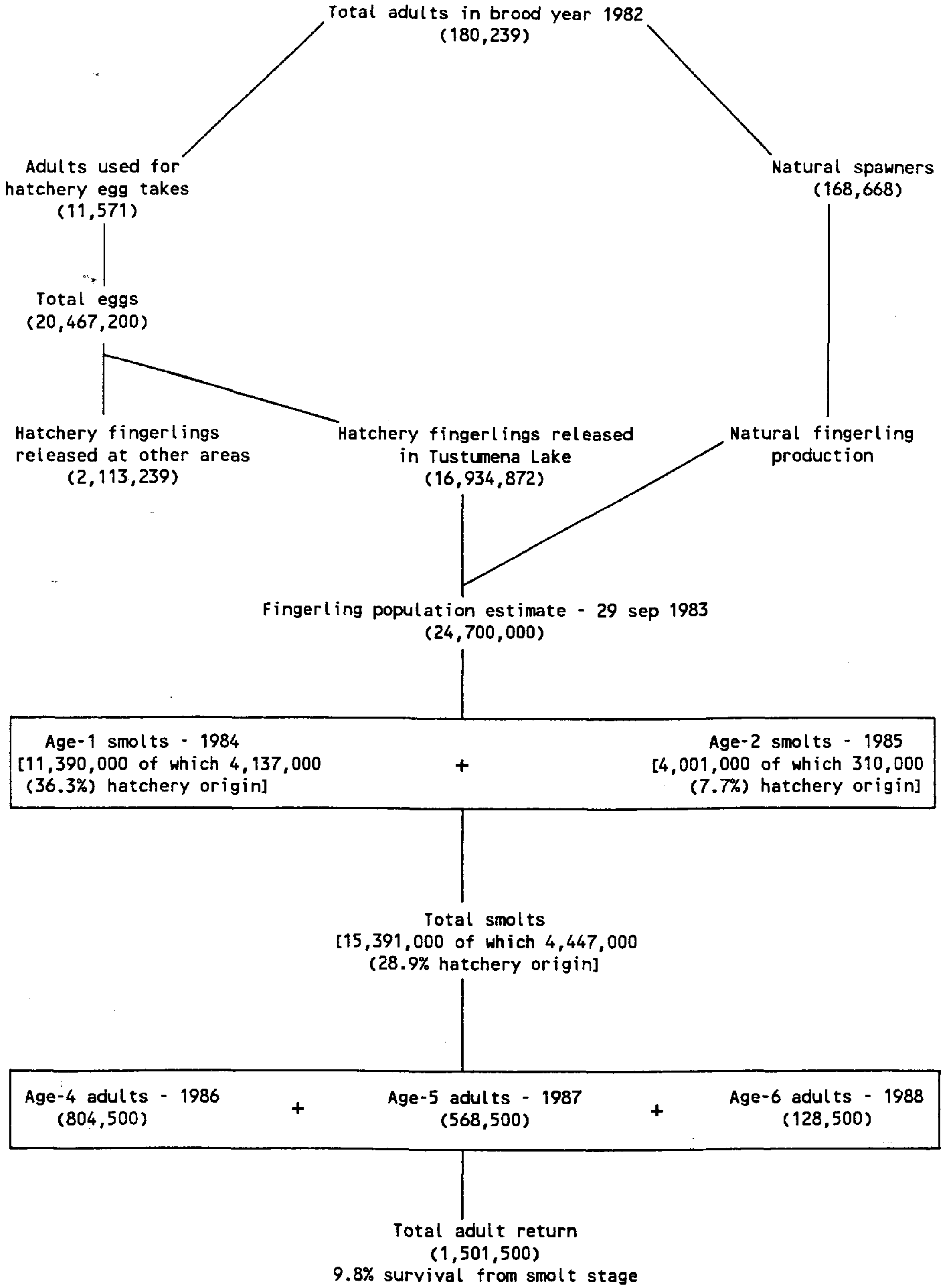


Figure A4. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1982.

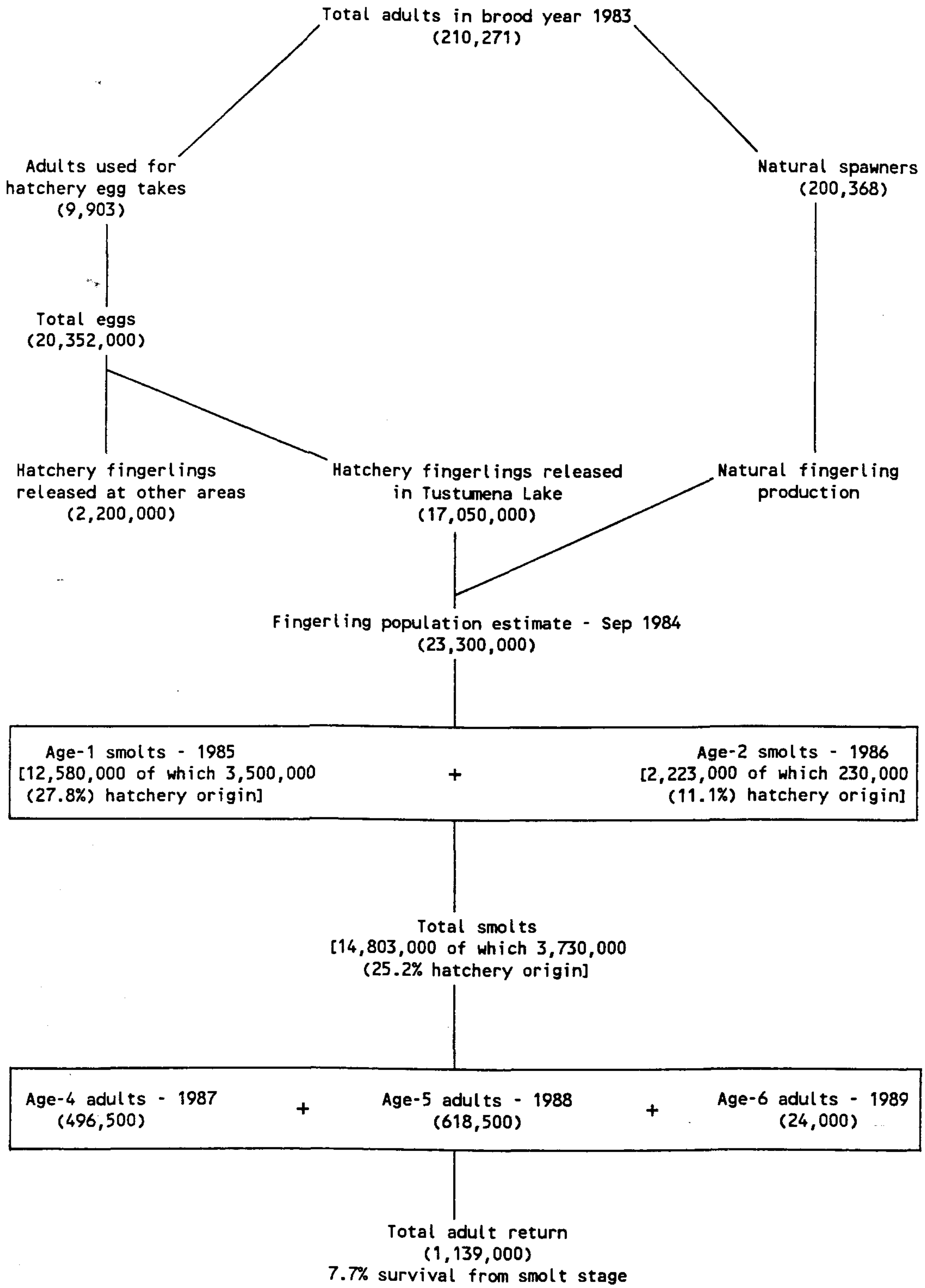


Figure A5. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1983.

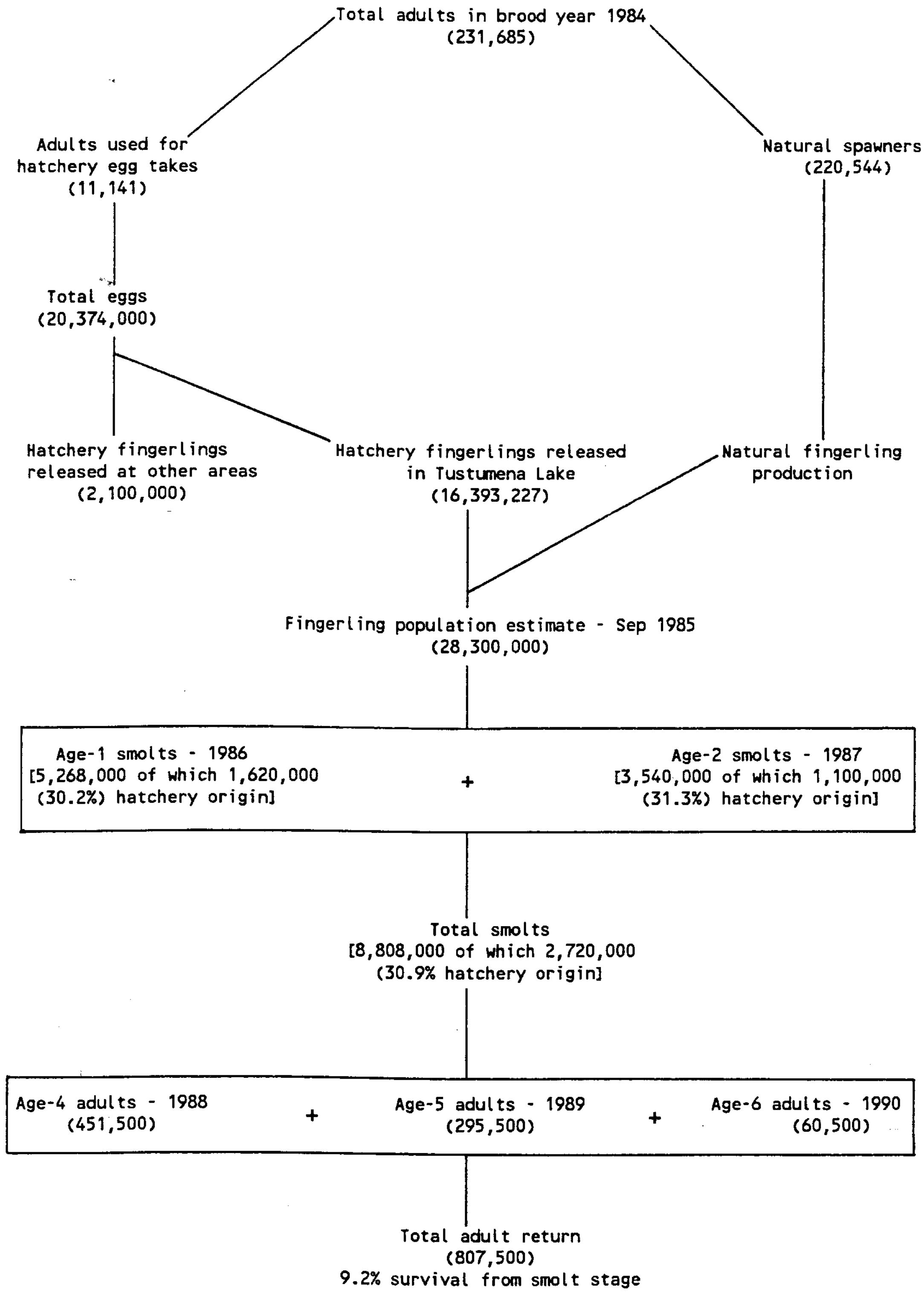


Figure A6. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1984.

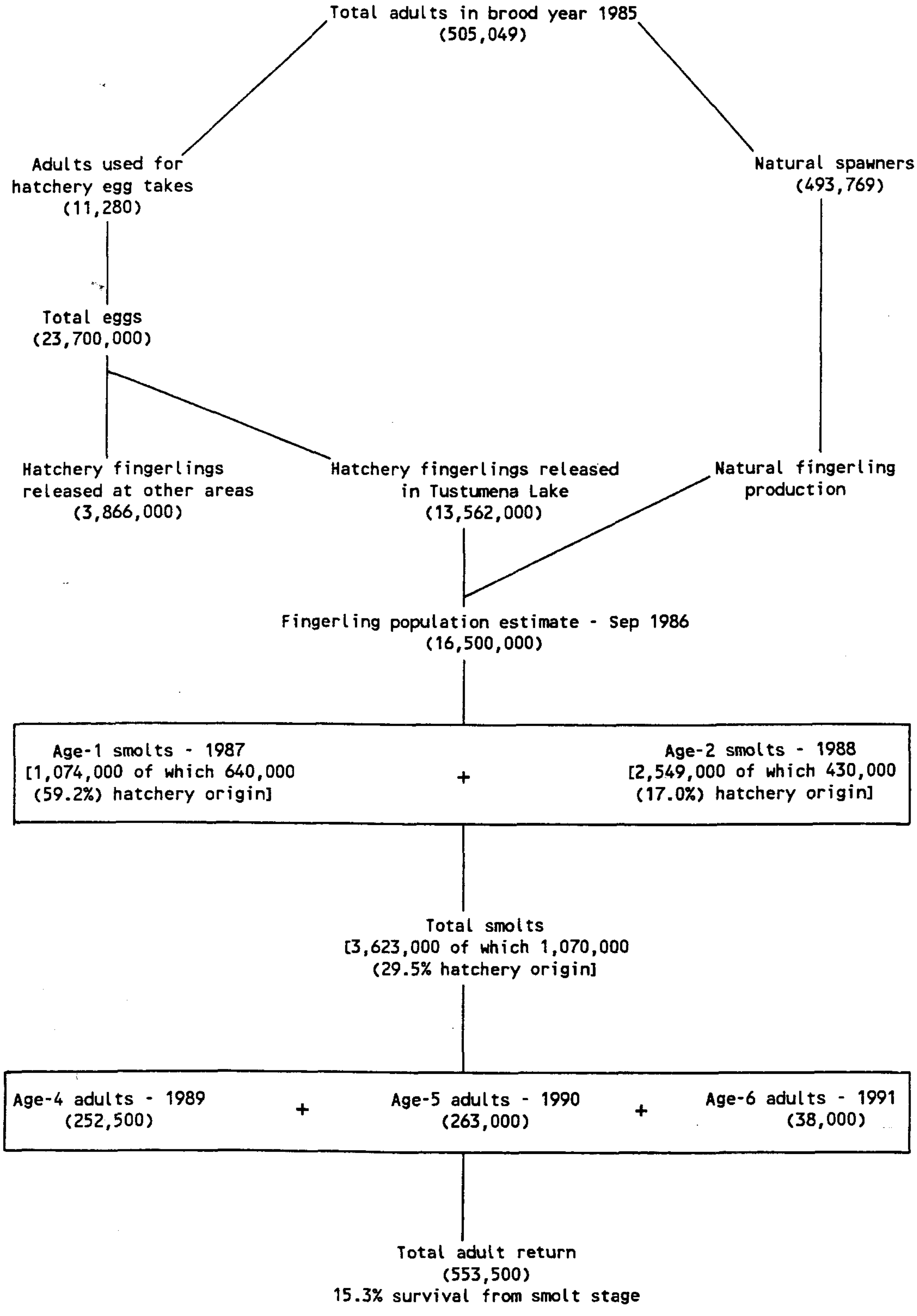


Figure A7. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1985.

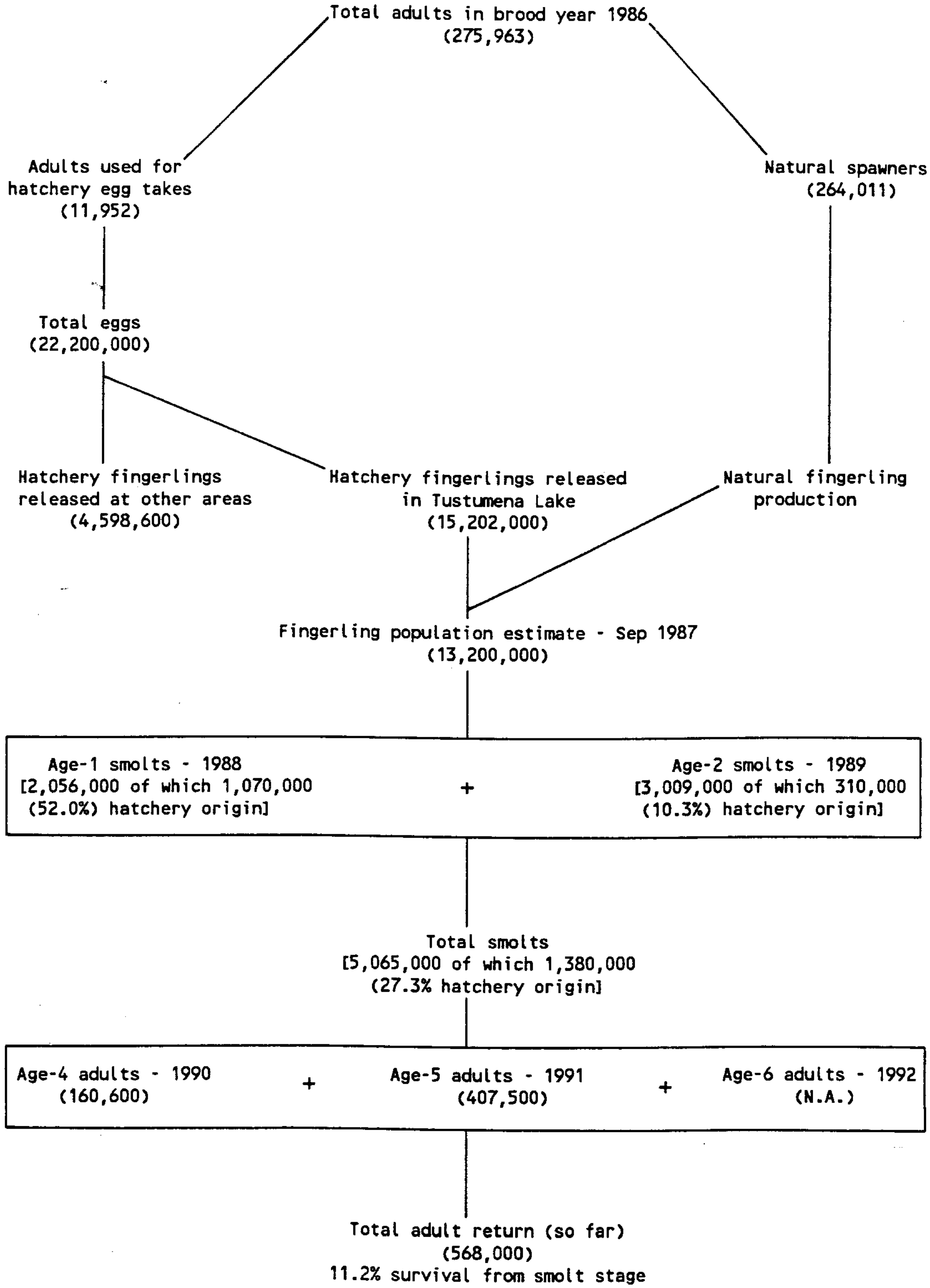
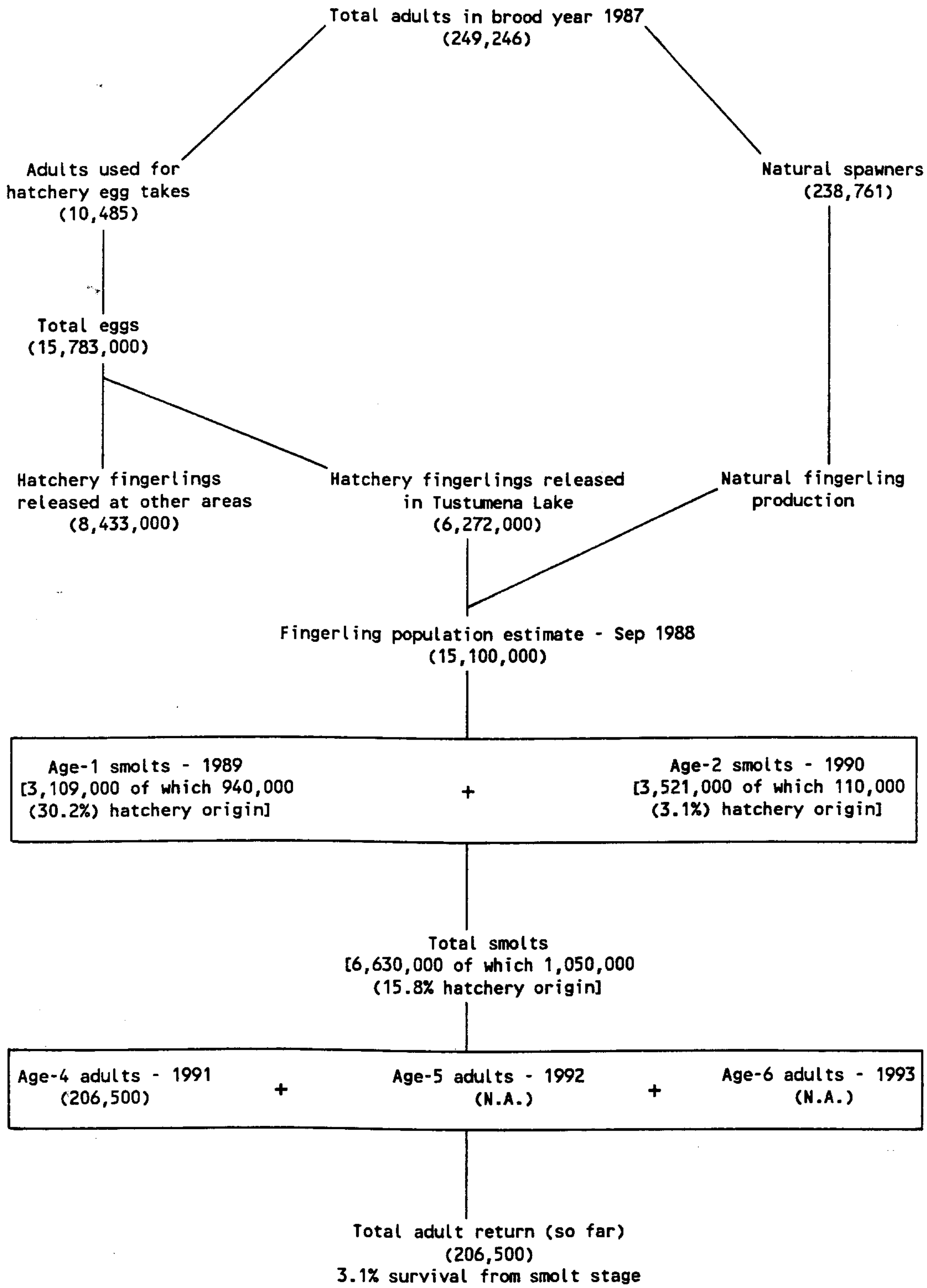


Figure A8. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1986.



Figur A9. Production of sockeye salmon in Tustumena Lake by life-history stage for brood year 1987.